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## INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL

A SURVEY OF THE PROBLEM OF EGG PRODUCTION AND A PRELIMINARY ANALYSIS OF AN EGG RECORD INTO ITS CONSTITUENT ELEMENTS

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### INTRODUCTION

A SURVEY of the problem of egg production, such as is made in the present paper, seems desirable at the present time because of the great interest taken in breeding for increased egg production. While the various factors discussed are familiar, to a degree at least, to most poultry keepers, nevertheless they are ignored in breeding practice and reliance placed upon the numerical record alone as a sufficiently detailed and accurate description of a hen's performance, although, as will be pointed out in a later section, identical numerical records result from quite diverse combinations of factors.

The point of view which we have been led to adopt may be stated in one form as follows: The *egg record* of a hen, expressed as a given number of eggs per unit of time and taken by itself, is not a sufficient measure or description of egg production, even under a favorable environment, for the record is the result of the interaction of a number of innate factors. Some of these factors, such as rate of growth, are quite distinct from egg production, while



others, such as rhythm, are almost inseparable from egg production itself. The numerical record of a hen shows only the number of eggs laid, but does not show the component elements which enter into the making of such a record. All these various elements must be studied individually and the influence exerted by each on egg production worked out. Moreover, the mode of inheritance of the separate factors must also be determined.

Further, it should be noted that the interrelation of the various factors is so complex that it is difficult to describe each by itself. In nearly all cases the bearing of some other factors must be considered to a certain extent, at least, along with that factor which is specifically under discussion.

It is important to observe that while the results obtained for the Rhode Island Reds described in this paper differ in several respects from those obtained by Pearl ('12) for Barred Plymouth Rocks, these differences are inherent in the birds themselves and are on a par with the visible differences, such as color, that exist between the two breeds. Pearl has anticipated that differences in fecundity in various strains and breeds are likely to be found. He states as follows:

The writer has no desire to generalize more widely from the facts set forth in this paper than the actual material experimentally studied warrants. It must be recognized as possible, if not indeed probable, that other races or breeds of poultry than those used in the present experiments may show a somewhat different scheme of inheritance of fecundity. . . . I wish only to emphasize that nothing is further from my desire or intention than to assert before such investigations have been made that the results of the present study apply unmodified to all races of domestic poultry.

It is clear, then, that a complete knowledge of fecundity and its inheritance in domestic birds can only be obtained by a careful study of egg production in all breeds and perhaps even in several strains of the same breed. As shown later on, one of the several factors that determine winter egg production is characteristic of Pearl's



Barred Plymouth Rocks, while another is characteristic of my Rhode Island Reds.

The data in this paper are obtained from a flock of 220 March and April hatched pullets placed in the laying houses in the fall of 1913, together with the data on winter egg production from the flock (numbering 482 pullets) placed in the laying houses in the fall of 1915, although the composition of this flock was not the same as that of 1913-14, because it had been altered by the addition of several other strains in order to overcome the unsatisfactory vitality of the original flock. The addition of new blood apparently increased the variability in some respects as shown by the statistical constants (*cf.* Figs. 1 and 2, also 10 and 10a). The winter production of the flock of 1914-15 was decidedly poor and apparently not normal, probably due largely to environmental conditions, and hence data from this flock have not been used.

It is impossible within the limits of this paper to present detailed data on all points discussed. To the reader who is unfamiliar with egg records, it may be said that an inspection of the records reveals the essential nature of the problems.

The original flock came mainly from one of the leading showroom strains of the country, to which were added a few individuals from another showroom strain. Neither strain, so far as known, had been especially bred for egg production, nor had any of the strains added in 1915.

#### WAYS OF MEASURING EGG PRODUCTION

It has been customary in times past to determine a hen's egg production by her record expressed in the number of eggs per year, the year usually running from November 1 through the succeeding October 31. At other times the first-year record of the hen has been taken as the time unit, beginning with her first egg and running 365 days therefrom. More recently, the Maine Experiment Station has used the period beginning with the first egg of a pullet and extending to March 1 as the unit of



measurement, since March 1 serves as a convenient calendar date, near the end of the winter cycle. Still more recently the same workers have suggested that even a shorter period would be desirable, because it is held that a hen only reaches her highest possibilities under favorable conditions. Recently the Utah Station (Ball, Turpin and Alder, '14) has suggested that for Leghorns the records be kept for three years, since hens that lay poorly the first year often lay much better during the second or third. Rice, however, ('13) has published data on this point, which show that such birds are the exception rather than the rule.

A year, however, may be considered to be a natural unit. During this period the whole cycle of seasonal changes is gone through with. Moreover, this period bears a definite relation to the bird's life cycle, for its beginning may be taken to correspond to the beginning of egg production in the fall, while its close roughly corresponds to the cessation of egg production the next fall, usually coinciding with the onset of the fall moult, though, of course, in some individuals, the biological year exceeds 365 days. Thus, the year would seem to mark a pretty definite period in the life of the bird as to her innate capacity for egg production. In this paper we have used both winter and annual periods as measures of production, as the necessities of the moment required.

There are some objections to each of the two common methods of determining the point at which the year begins. If the year begins with the first egg of each individual, the differences in age at which the first egg is produced are neglected. If a given point in the year is chosen and the production of all individuals within a year from this date recorded, differences in time of hatching are neglected. Possibly a more satisfactory method would be to take 365 days from the beginning of egg production in each flock of equal age, or else from the average date at which production begins.

The terms "high producer" and "low producer" are



frequently encountered, but each is used very loosely. The use, either of the term "higher producer" or "low producer" without qualifications of any sort can scarcely be considered sufficiently precise. Unless qualified by the word annual, the term "high producer" in this paper will be understood to refer to the winter record only. Pearl ('12) has defined a high producer as a bird that lays over 30 eggs during the winter, a mediocre producer as one that lays during the winter but that lays fewer than thirty eggs, while a zero producer does not lay at all during the winter. As will appear later, the use of the numerical value of the record as its sole characteristic is insufficiently precise. The term "true mediocre producer" will be used to denote a mediocre producer in the sense (Pearl's) explained below, while the term "mediocre (under 30 eggs) producer" will be used elsewhere.

*The Influence of External Factors.*—A brief consideration of the relation of external factors to egg production is necessary before considering internal factors.

External factors may be divided into two classes: first those that operate rather directly upon egg production, and secondly those that operate indirectly, through their influence on the organism as a whole.

Under the head of direct factors should be mentioned housing, climate, food, general care, etc. It should go without saying that the birds must be properly fed and kept under conditions generally recognized as suitable for maximum egg production. It is not yet clear, however, that the optimum conditions are fully known, or that they can be obtained at will, for with the present appliances for keeping poultry, only the crudest sort of approximation can be made toward securing a uniform environment. For example, one is never certain with open-front houses that a draft may not strike one portion of the flock, while on the roosts, but not another. There are many little things of this sort which can not at present be controlled, nor is it definitely known in what way these "little things" influence egg production. Some



appear to be without any influence whatsoever; others appear to be of varying degrees of importance.

Thus, it is not easily possible to overemphasize the importance of the environment in relation to egg production. At best, certain elements of the environment are partially controlled and *similar* conditions supplied to the members of the flock under experimentation, but it is impossible with the best practical facilities at present available to furnish *identical* conditions to all individuals of the same flock. At the very best one can only go through the motions of providing such conditions. Moreover, one may be forced to modify the procedure selected in order to keep the birds in good condition. Furthermore, *individuals* or *strains* may not react in the *same* fashion to *identical* conditions.

The difference in the reaction of individuals of the same strain to similar conditions, particularly when these conditions fall near the critical point for the strain (or species), is a matter of considerable importance, especially when a character such as egg production is under study, and more especially when it is impossible to control certain important elements of the environment. As long as the environment is not too far from the optimum, birds of low vitality, for example, may do quite as well as birds of much higher vitality, but when the environment approaches either end of its range, then its effects begin to manifest themselves.

A full discussion of the possible influence of the environment, either directly or indirectly, upon egg production as a whole or upon any of the several factors influencing production is outside the scope of this paper. While the reader should bear in mind the possibility that the environment has introduced disturbing factors, every effort has been made to keep all controllable elements, such as feeding and housing uniform.

Turning now to internal factors, we find that these also may be considered under two heads. We have little to do with the factors falling under one of these heads, for



their effect is exerted only indirectly. They undoubtedly play an important part in egg production, but like many external factors they are without influence unless they fail in some way. Such factors are the capacity to digest and assimilate food, to excrete waste matters properly, etc. It is not my purpose at this time to discuss such factors. Those internal factors with which we are mostly concerned are those whose relations to egg production are much more obvious. They are rate of growth of the chick, cessation of growth, the attainment of both bodily and sexual maturity, moults, the size of the bird, the stamina of the bird, the presence or absence of cycles, litters or clutches of production, the rhythm of production, the rate of production for definite time intervals, age at first egg, and broodiness. Some of them are clearly separable from egg production. Others are so closely interwoven that it is impossible to say that they are not phases of egg production. Whether or not this is so, is of no immediate importance from the standpoint of inheritance, since the result will probably be the same whether they are treated as genetic factors that are separable from egg production or treated as groups into which egg production itself may be divided. These factors may be regarded as phases of egg production if one desires, but on the whole it has seemed profitable to regard them as factors influencing egg production.

*Rate of Growth, Bodily Maturity, Cessation of Growth,  
Sexual Maturity<sup>1</sup>*

These interrelated factors are closely interwoven in their effect on egg production. Under normal conditions it is clear that sexual maturity is indicated by the beginning of egg laying, and may be measured by a bird's age at her first egg, i. e., the length of time elapsing between the date hatched and date of first egg. Sexual maturity, however, demands certain antecedent conditions before it can become manifest. Among other conditions is a cer-

<sup>1</sup> Unless otherwise stated, reference here is to the female only.



tain body size, which depends upon the rate at which the individual grows, as well as the limiting size for that individual. That is, size at a given age is the result of rate multiplied by time, up to certain limiting values determined by the genetic composition. Cessation of growth, however, does not necessarily coincide with the onset of sexual maturity nor even with general bodily maturity. Although it is certain that the hen is heavier in her second autumn than at the beginning of egg production, our data show that there is little or no growth during the first winter. We must, then, distinguish between sexual maturity, which is capable of manifesting itself as soon as the body reaches a certain size, from that maturity which is not attained until long after the adult size is reached. At present the relation between sexual maturity and bodily maturity has not been worked out. Some extreme phases, however, of the interrelation appear *a priori* probable. Chicks that grow very rapidly naturally tend to reach sexual maturity at a very early period in their life. They may or may not start in laying immediately after reaching full size. Other birds grow very slowly and can not lay before a certain size is reached. Therefore, they must of necessity reach sexual maturity relatively late in life. It may be impossible for birds of this sort to reach sexual maturity before spring if hatched during the usual breeding season (April, May). The general effect of slow growth, then, will be to lower the record made by such individuals, although they may be otherwise identical with those that grow more rapidly.

Combined with the factors mentioned are the factors that limit the size finally reached. As pointed out above, size results from rate of growth times length of period through which growth continues. Each factor is determined in part by the environment and in part by the genetic constitution of the bird.

The following combinations of factors (Table I) and their effect on egg production may be *assumed*. Each factor is treated as though it were wholly independent



of the others. Early sexual maturity is assumed to be a constitutional tendency to begin laying as soon as a sufficient body size or body maturity is reached, while late sexual maturity is assumed to be a tendency to delay production until after body maturity is attained. This heading, however, does not refer to the objective attainment of sexual maturity which is shown by the column on "time of first egg." The length of the growth period also is assumed to be determined by the attainment of bodily maturity.

TABLE I

VARIOUS COMBINATIONS OF HYPOTHETICAL GROWTH FACTORS WITH THEIR EFFECT ON WINTER EGG PRODUCTION

Rate of Growth	Sexual Maturity	Growth Period	Probable Time of First Egg	Probable Winter Egg Production
Rapid	Early	Short	Early	High
"	Late	Short	Late	Low
"	Early	Long	Relatively late	Medium
"	Late	Long	Late	Low
Slow	Early	Short	Relatively late	Medium
"	Late	Short	Relatively late	Low
"	Early	Long	Late	Low
"	Late	Long	Very late	Zero

It appears from this table that early sexual maturity can become fully effective only when combined with rapid growth during a short growth period.

The effect of the activities of some of these factors as bearing on winter egg production may be given more specifically as follows: If we measure egg production by the number of eggs laid before the 1st of March, assuming for the moment that this point represents, approximately at least, a definite point in the history of the egg production of each individual, it follows that the birds hatched during April and May, or to take a definite point for the purposes of illustration—April 15—which mature at five months, as is sometimes the case, will begin to lay September 15 and will lay a large number of eggs before March 1, provided, of course, that they do not moult. On the other hand, true mediocre productivity (slow rate) associated with early maturity will tend to force a bird



out of the class of mediocre producers, when measured by a specific number of eggs, into that of the high class. If, then, one is dealing with a flock in which these degrees of maturity exist, it is evident that extreme care must be taken to avoid confusion due to differences in maturity or rate of growth.

Differences in maturity may be observed among the males as well as the females, although there is no precise objective point at which a male may be said to have become mature, which is comparable to the first egg of a pullet. On the whole, the larger birds tend to mature later than the smaller, though the rule is by no means rigid, since some small birds grow slowly while some large birds grow quickly. Since age at first egg is so large a factor in determining the kind of record a bird makes, one has a physiological character in the male of considerable value as an index of his capacity for producing females that will mature at a given age.

The age of a bird when she produces her first egg does not coincide necessarily with bodily maturity, theoretically at least, although it seems that a certain size must be reached before the bird can begin to lay. On the other hand, the relation between body size and age at first egg as frequently encountered is of a sort such that the larger birds tend to lay at a later absolute age than the smaller ones hatched the same day. There are many exceptions, however, to this rule. It would, perhaps, be better expressed to say that more heavy birds lay late in life than early, while more of the lighter birds lay early than late. For one of the flocks, the coefficient of correlation between age at first egg and weight has been calculated and found to have a value of  $+ .5473 \pm .0216$ .

The influence of the date at which the first egg is produced as well as the relation of age at first egg to the number of eggs laid during the winter months is shown in the series of records shown in Figs. 3 and 4 (Page 78). These records have been selected in such a way that the rate of production is nearly constant, although the date of hatch-



ing of the individual birds covers a period of five weeks. The records are to be read as follows: The number in the upper left-hand corner is the hen's number. The *vertical* mark in *each* square indicates that an egg was produced on that day. The totals are given for each month while the figure at the extreme right of the row headed

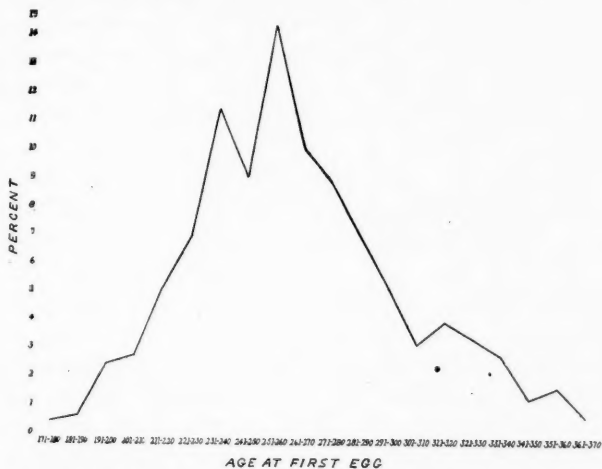


FIG. 1.<sup>8</sup> Graph showing the percentage of the flock beginning to lay at the age (in days) indicated by the class limits. Flock hatched in March, April and May, 1915.  $M = 263.19$ ,  $S. D. = 37.71$ ;  $C. V._2 = 43.00$ ,  $C. V._1 = 14.33$ .

"February" is the total number of eggs for the winter period. The records for March and April have also been included in order to show the type of record made by birds that begin to lay very late in the season. These records show clearly that no sharp dividing line exists in the number of eggs laid. On the contrary, it is clear that birds hatched at the same time begin to lay at widely different dates and that in consequence differences in egg yield for the winter period result. That this result is of general applicability to our flocks is shown by the fair

<sup>8</sup> In calculating the  $C. V._{(2)}$  for the data given in Figs 1 and 2, the mean was taken as the difference between the mean age and the lower end of the range of Fig. 1.



amount of homogeneity in the flocks in respect to rate of production as described below.

Graphs showing the age at first egg for the flocks of 1913-14 and 1915-16 are shown in Figs. 1 and 2. The former (Fig. 2) is unimodal and has a narrow base, the shape of the curve indicating a high degree of homo-

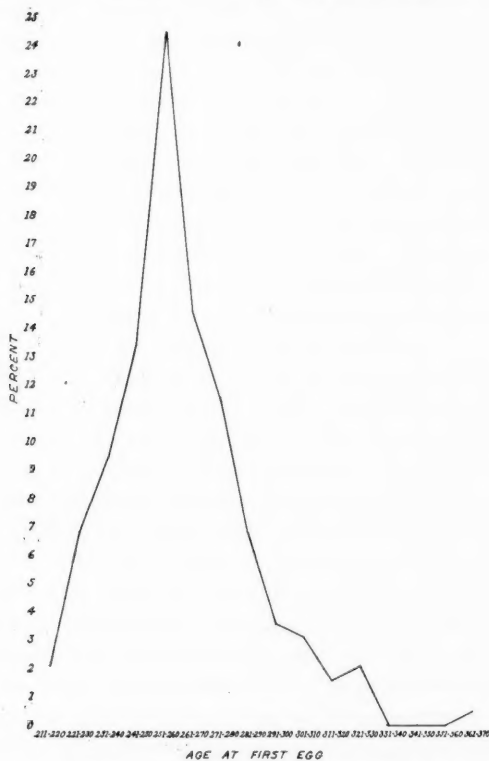


FIG. 2\* Graph showing the percentage of the flock beginning to lay at the age (in days) indicated by the class limits. Flock hatched in March and April, 1913.  $M = 261.18$ ,  $S. D. = 24.34$ ,  $C. V. = 28.41$ ,  $C. V. = 9.32$ .

geneity in the flock. As might be expected from the nature of the data (which is affected by the environment in only one direction, *i. e.*, toward a retardation of the age at first egg) the lower part of the right-hand side slopes



off more gradually than the left. The mean has a value of 261.18 days.<sup>2</sup>

The curve for the flock of 1915-16 (Fig. 1) is somewhat unlike the preceding. It is distinctly bimodal, but it is not altogether clear that this bimodality indicates two genotypes, for it may be due to chance alone. The base is broader than for the 1913-14 curve, indicating less homogeneity of the flock in this respect, although the same gradual slope on the right-hand side is apparent. There are reasons, however, for believing that the left-hand side of the graph for the flock of 1913-14 was shortened by the methods of handling the pullets that fall. The mean has a value of 263.18 days. The difference between this graph and the first is undoubtedly due to the changes in the composition of the flock as described in an earlier paragraph.

Graphic representations of the day on which the various members of the flock produced their first egg are shown in Figs. 5 and 6. The data for the two flocks, *i. e.*, 1913-14 and 1915-16, are divided into groups according to the month in which the pullets were hatched. Each dot in the figure represents the first egg of a pullet and is placed in a square corresponding to the date on which the egg was laid. If more than one pullet began to lay on a given date, there is a dot for each pullet.

There are some interesting differences and resemblances between the groups mentioned in the distribution of the first egg through the various months. In all instances the pullets laying for the first time come in slowly during the first few weeks. Then follows a period of six to eight weeks during which the new pullets come in at a faster and fairly uniform rate. This period is followed by a third period when new pullets come in slowly, the last of the period representing the stragglers. The fairly uniform scatter is due in part to the inclusion of several

<sup>2</sup> In this paper we have given only those statistical constants that appear to be particularly pertinent and as a rule have omitted the probable error, especially where "n" is large, unless there has been special reason for inserting it.



No. 4846

HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 191 DAYS

Date 1915-16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
Sept.....																												/	/		■	2
Oct.....	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/		/	/	/	22	
Nov.....	/		N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	N	/	/	/	■	20	
Dec.....		N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	21	
Jan.....	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	22	
Feb.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	■	■	20	
																															107	
Mar.....	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	18	
Apr.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/		N						N		N	N	N	■	14	

No. 4921

HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 219 DAYS

Date 1915-16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
Sept.....																															■	0
Oct.....																									/	/	/	/	/	/		3
Nov.....	/	/	/	/	/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	■	17	
Dec.....	/	/		/	/	/	/	/	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	24	
Jan.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	22	
Feb.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	■	■	18	
																															84	
Mar.....	/	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	27	
Apr.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	■	28	

FIGS. 3 AND 4. Daily records of Rhode Island Red pullets hatched in 1915, arranged in order of decreasing total winter eggs to show the effect of approximately equal rates of production, but of different dates of first egg on the total winter production, as shown by the numeral at the right of the February record. March and April records are included to show that no fixed date can be selected as a dividing line. 1 = an egg; N = on nest but did not lay; B. L. = removed to broody coop; A = returned to pen.



## HATCHED MARCH 7, 1915. AGE AT FIRST EGG, 266 DAYS

Date 1915-16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
Nov.....																								N			N	/	/		2	
Dec.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	20	
Jan.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	21	
Feb.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	20	
																															63	
Mar.....	/	/	/	/	/	/	/	/	/	/	N.	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	23	
Apr.....	/	/	/	/	/	/	/	B				A	N				/	/	/	/	/	/	/	/	/	/	/	/	/	/	17	

## HATCHED APRIL 11, 1915. AGE AT FIRST EGG, 268 DAYS

Date 1915-16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
Nov.....																																0
Dec.....																																0
Jan.....				/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	21	
Feb.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	20	
Mar.....		/	/		/	/	/	/	/	/	/		N	/	/	/	/	/	/	/	/	/	/	/	/	/	BL	/		20	41	
Apr.....	A		N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	BL	/		A	BL			A					14	

FIGS. 3 AND 4.—Continued.



HATCHED MARCH 14, 1915. AGE AT FIRST EGG, 312 DAYS

HATCHED MARCH 14, 1915. AGE AT FIRST EGG, 312 DAYS																																	
No. 4620	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals	
Date 1915-16																																	
Nov.....																																	0
Dec.....																																	0
Jan.....									/							/	/	/		/	N			/	/	/	/	/	/	/	/	12	
Feb.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	23	
																																	35
Mar.....		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	26	
Apr.....	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	24	

HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 294 DAYS

HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 294 DAYS																																		
No. 5180	Date 1915-16		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
Nov.....																																		0
Dec.....																																		0
Jan.....																								/	/	/	/	/	/	/	/	/	7	
Feb.....	/		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	22	29	
Mar.....	/	/		/	/	/	/	N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	BL			21		
Apr.....	A	N	N					/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	N		20	

FIGS. 3 AND 4.—Continued.



HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 304 DAYS

HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 304 DAYS																																	
No. 5149	Date 1915-16	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
	Nov.....																																0
	Dec.....																																0
	Jan.....																																0
	Feb.....		/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	21	
	Mar.....	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	21	
	Apr.....	/	/	/	/	/	/	N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	28	
																																	24

HATCHED MARCH 14, 1915. AGE AT FIRST EGG, 336 DAYS

HATCHED MARCH 14, 1915. AGE AT FIRST EGG, 336 DAYS																																
No. 4568	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
Date 1915-16																																
Nov.....																																0
Dec.....																																0
Jan.....																																0
Feb.....												/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	12	12
Mar.....	/	/	/	/	/	/	/	/	/	N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	26
Apr.....	N	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	N	/	/	/	/	/	/	/	BL	/	23	

FIGS. 3 AND 4.—Continued.



HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 334 DAYS

[illegible]

HATCHED APRIL 4, 1915. AGE AT FIRST EGG, 352 DAYS

[illegible]

**FIGS. 3 AND 4.—Concluded.**

HATCHED IN MARCH. 1915.



HATCHED IN MARCH, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.....	.				.			.				..			.	.	.						.	.	.	.	.	.	.	.	.	8.3
Oct.....	.	.	.	.			.	.	..		.	.	.	.	.		...				.	.	.	.	.	.	.	.	.	.	.	13.9
Nov.....	.	...	...	...	..	..		.	..	.	..	.	...	...	.	...	..	.	.	..	..	..	.	.	.	.	.	.	.	.	.	27.2
Dec.....	...	.	.	.	.	...	...	...	..	...	...	.	...	...	.	.	.	.	..	.	.	.	.	.	.	.	.	.	.	.	.	24.4
Jan.....	.		..				...	.	..	.	.					.	.	.	.								.	.	.	.	.	12.2
Feb.....	..		.	..		.		.	.	.	.	.	.	.	.	.			.	.	.	.				.	.	.	.	.	.	8.9
Mar.....			.				.	.	.				.	.			.	.	.	.	.	.				.	.	.	.	.	.	3.9
Apr.....	.																						.	.								1.1

HATCHED IN APRIL, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.....																																1.1
Oct.....																..	..	..		..							..	..				14.5
Nov.....					.	..	..	.	.	.	.	...	.	.	...	...	...	...	...	..	..	..	..	..	..	..	..	..	..	..	..	34.6
Dec.....	.	.	...	...	...	...		.	.	..	...	...	...	.	...	...	.			..	..	..	..	..	..	..	..	..	..	..	..	25.7
Jan.....	..	...	..	...	...	...		.	.	.	.	..	..	.	.	...	.	...	...	.	.	.	.	.	.	.	.	.	.	.	.	12.8
Feb.....	.	...	.	.			.	.	.	.	.	..		.	.	.	.	.	...							.	.	.	.	.	.	10.1
Mar.....	.		...				.	...	...	...			.	.	.	.					.	.				.	.	.	.	.	.	1.1
Apr.....	...									.																	.					1.1

Fig. 5.



## HATCHED IN MAY, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.....																																
Oct.....																																
Nov.....																																
Dec.....																																
Jan.....																																
Feb.....																																
Mar.....																																
Apr.....																																

FIG. 5.—*Concluded.* Diagram to show the date on which the first egg of each member of the flock was laid. Flock of 1915-16.



hatches on one chart, and also to the ungrouped data, for if the data be grouped in 10-day periods, a curve is ob-

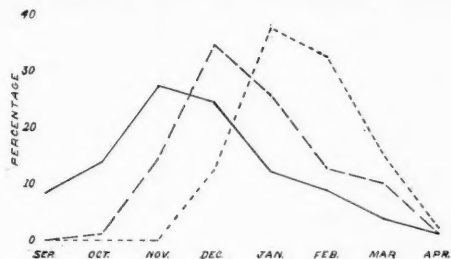


FIG. 5a. Graph showing the percentage of the flock of 1915-16 that began to lay in the month indicated. From Fig. 5. — March, - - - April, and . . . May hatched pullets, respectively.

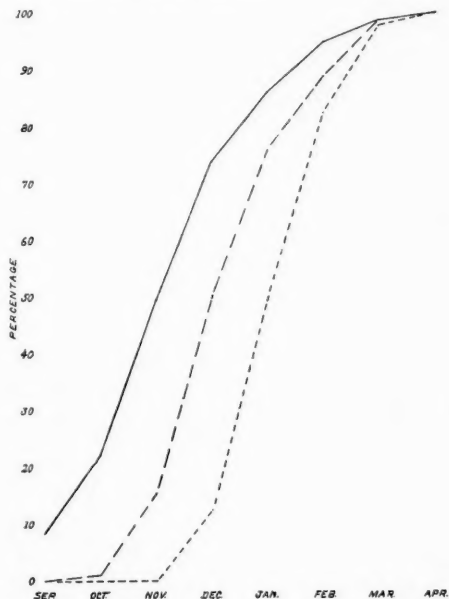


FIG. 5b. Graph showing the percentage of the flock of 1915-16 that began to lay during or before the month indicated. From Fig. 5. — March, - - - April, and . . . May hatched pullets, respectively.

tained similar to the one that results from the combination of the age at first egg curves of several consecutive hatches.



## HATCHED IN MARCH, 1913

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.	
Sept.....																																	
Oct.....																																	
Nov.....											*		*			**		*										*	**	*		18.5	
Dec.....	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	58.5
Jan.....			*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	15.4	
Feb.....	*							*						*		*																6.2	
Mar.....															*																	1.5	
Apr.....																																	

## HATCHED IN APRIL, 1913

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.....																																
Oct.....																																
Nov.....												*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	16.5
Dec.....					*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	38.6
Jan.....	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	35.4
Feb.....	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	8.7
Mar.....	*																															0.8
Apr.....																																

Fig. 6.



HATCHED IN MAY, 1913

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.....																																
Oct.....																																
Nov.....																																
Dec.....																																
Jan.....																																
Feb.....																																
Mar.....																																
Apr.....																																

Fig. 6.—*Concluded.* Diagram to show the date on which the first egg of each member of the flock was laid. Flock of 1913-14.

HATCHED MARCH 22, 1915

Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Per Cent.
Sept.....																																
Oct.....																																
Nov.....																																
Dec.....																																
Jan.....																																
Feb.....																																
Mar.....																																
Apr.....																																

Fig. 7. Diagram to show the date on which the first egg of each member of the flock was laid. This figure is based on a new sample of the original strain that made their winter record in 1913-16. See text.



In any one hatching group a period of several months elapses between the date the first pullet begins to lay and the date the last member of the flock starts. This period is longest for the March-hatched birds, apparently because the warm spring weather brings all the stragglers to laying and because the March-hatched birds are the first to lay in the fall. For the May-hatched birds the period between first and last pullet is shorter because they begin to lay later in the fall than the March-hatched birds.

For the March-hatched pullets of 1915-16, the initial period is nearly twice as long as for the April or May pullets. The date of the first egg of the first pullet is approximately a month later for the May than for the April pullets. The data, however, for 1913-14 are not quite comparable with those for 1915-16. In the first place it was impossible in 1913, because of lack of room, to begin putting the pullets into the laying quarters until late in October, while some were not finally in place until about the middle of November. The birds therefore did not get settled down at once. The March- and April-hatched pullets both began to lay at approximately the same time and although most (77 per cent.) of the March birds had commenced laying by January, a considerable percentage (viz., 44.9 per cent.) of the April pullets did not begin to lay until after January 1, which is approximately the same percentage (viz., 49.7 per cent.) obtained for the April pullets of the 1915-16 flock. It should be noted, too, that 73.9 per cent. of the March pullets of this year began to lay before January 1, so that the effect of the delay in housing the 1913-14 flock shows itself principally in a retardation of the first eggs of the March pullets, forcing a larger percentage of first eggs into December than would be normal for that flock. There is a further difference in the two years. The percentage of the April hatched pullets laying after February 1 was about  $2\frac{1}{2}$  times as great for the 1915-16 flock as for the 1913-14 flock, the ratio being 24 per cent. for the former to 9.5 per cent. for the latter.



There is another way in which the close relation between age at first egg (also date of first egg) and the winter egg record can be shown, for it follows that the higher the age at first egg the lower the winter record

TABLE II

AVERAGE WINTER EGG PRODUCTION FOR EACH WINTER MONTH OF 1915-16,  
BY HATCHES

Date Hatched, 1915	Number Pullets in Hatch	Average Winter Pro- duction	August	Sep- tember	October	No- vember	De- cember	January	Feb- ruary
February 7...	12	66.83	5.9	14.3	11.9	5.2	2.6	10.8	16.2
February 14...	8	56.63	5.3	9.9	8.8	6.6	5.5	9.4	11.3
February 21...	13	65.92	1.8	10.5	10.9	10.1	8.8	10.8	13.1
February 28...	18	41.44	0.0	2.0	3.7	6.3	8.8	9.4	11.3
March 7.....	24	44.88	0.0	1.5	5.2	7.2	10.6	10.6	9.9
March 14.....	33	34.15	0.0	0.0	0.8	5.1	7.7	8.3	12.2
March 21.....	48	40.67	0.0	0.3	2.7	7.2	11.6	9.9	8.9
March 28.....	17	40.00	0.0	0.0	0.0	4.4	11.8	12.5	11.3
April 4.....	29	29.31	0.0	0.0	0.1	1.0	8.0	9.4	10.7
April 11.....	63	31.30	0.0	0.0	0.0	1.9	6.8	10.9	11.8
April 18.....	47	29.26	0.0	0.0	0.0	0.6	5.9	10.4	12.4
April 25.....	34	27.35	0.0	0.0	0.0	0.4	3.3	10.6	13.1
May 2.....	30	20.27	0.0	0.0	0.0	0.0	1.3	6.9	12.0
May 9.....	30	20.37	0.0	0.0	0.0	0.0	1.8	7.0	11.6
May 16.....	19	18.95	0.0	0.0	0.0	0.0	0.1	4.3	14.6
May 23.....	37	17.78	0.0	0.0	0.0	0.0	0.2	4.6	12.9
May 30.....	20	11.35	0.0	0.0	0.0	0.0	0.3	3.1	8.0

should be. In calculating this coefficient of correlation it is necessary that the birds should all be hatched at the same time, so that for our flocks, which were hatched at intervals of one week, it would be necessary to form as many correlation tables as there were hatches. The probable results did not seem to warrant the labor involved, at

TABLE III

AVERAGE WINTER EGG PRODUCTION FOR EACH MONTH OF 1915-16, GROUPED  
BY MONTH HATCHED

Month Hatched, 1915	Number Pullets	Average Winter Pro- duction	August	Sep- tember	October	No- vember	De- cember	January	Feb- ruary
February.....	51	56.2	2.7	8.3	8.3	7.1	6.8	10.1	12.9
March.....	122	39.8	0.0	0.4	2.3	6.2	10.4	10.0	10.3
April.....	173	29.8	0.0	0.0	0.02	1.1	6.1	10.5	12.0
May.....	136	18.1	0.0	0.0	0.0	0.0	0.8	5.4	11.9



least not at present, so that the coefficient was calculated for one of the largest hatches only. The value found,  $r = -.829 \pm .029$ , is in full agreement with the hypothesis that the winter egg production of a flock all hatched at the same time, depends largely upon the age at which the first egg is produced.

TABLE IV

AVERAGE WINTER EGG PRODUCTION FOR EACH WINTER MONTH OF 1913-14,  
BY HATCHES

Date Hatched, 1913	Number Pullets in Hatch	Average Winter Pro- duction	August	Sep- tember	October	No- vember	De- cember	January	Feb- ruary
March 9.....	10	53.3	.....	.....	.....	3.7	12.7	18.6	18.3
March 16.....	12	44.8	.....	.....	.....	1.6	11.3	16.8	15.1
March 23.....	22	47.1	.....	.....	.....	0.3	10.3	19.4	17.1
March 30.....	17	36.5	.....	.....	.....	0.0	7.7	13.9	14.9
April 6.....	29	48.6	.....	.....	.....	2.4	11.4	18.0	16.9
April 13.....	19	41.2	.....	.....	.....	1.2	8.4	16.1	15.6
April 20.....	37	35.2	.....	.....	.....	0.2	3.3	15.9	15.8
April 27.....	40	32.5	.....	.....	.....	0.1	4.1	12.5	15.9
May 4.....	9	42.2	.....	.....	.....	0.0	4.0	19.6	18.7
May 11.....	13	25.2	.....	.....	.....	0.0	1.3	8.6	15.3

TABLE V

AVERAGE WINTER EGG PRODUCTION FOR EACH MONTH OF 1915-16, OF STOCK  
FROM ORIGINAL SOURCE

Date Hatched, 1915	Number Pullets in Hatch	Average Winter Pro- duction	August	Sep- tember	October	No- vember	De- cember	January	Feb- ruary
March 22.....	35	41.11	0.0	0.0	2.3	4.2	7.9	12.8	13.9
April 27.....	16	23.31	0.0	0.0	0.0	0.0	2.6	8.4	12.3

TABLE VI

A COMPARISON OF THE PROPORTION OF THE FLOCK LAYING EITHER MORE OR LESS THAN 30 EGGS DURING THE WINTER, TOGETHER WITH THE MEANS OF THE RESPECTIVE GROUPS, GROUPED ACCORDING TO THE MONTH HATCHED. THE ZERO PRODUCERS HAVE BEEN OMITTED AND ALSO THE FEW BIRDS THAT LAID EXACTLY 30 EGGS

Month	Over 30			Under 30		
	Av. Winter Production	Number Individuals	Per Cent.	Per Cent.	Av. Winter Production	Number Individuals
February.....	63.0	43	84.3	15.7	18.8	8
March.....	54.9	77	68.8	31.3	16.4	35
April.....	46.3	88	58.7	41.3	16.0	62
May.....	40.5	29	26.6	73.4	16.1	80



The influence of the time of hatching on winter egg production is shown in Fig. 8 and Table II and III based on the records for 1915-16. The lower graph in Fig. 8 is for birds hatched in March; the middle graph for birds hatched in April; while the upper is for the May-hatched birds. Similar data for 1913-14 are given in Table IV.,

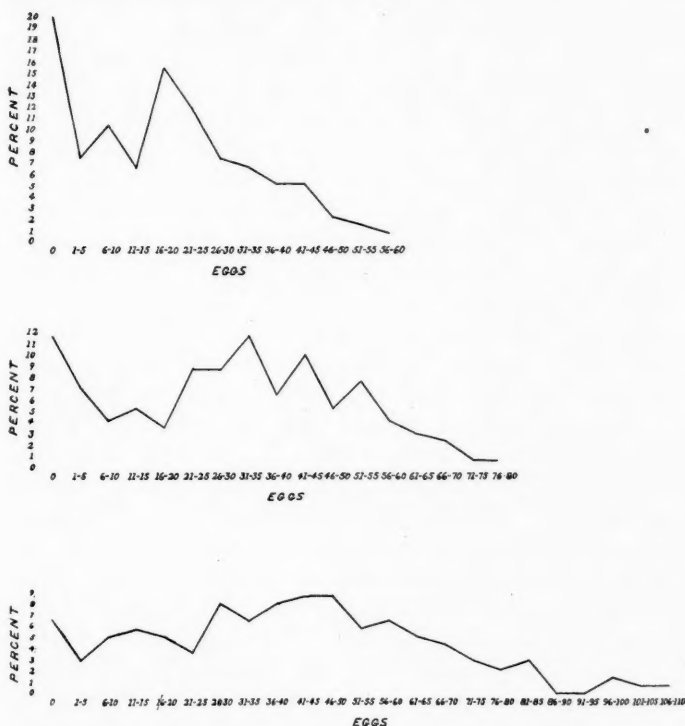


FIG. 8. The effect of time of hatching on winter egg production, the graph showing the per cent. of flock laying the specified number of eggs for the winter period of 1915-16. Lower curve, pullets hatched in March, 1915. Middle curve, pullets hatched in April. Upper curve, pullets hatched in May. M. for March = 42.65, April = 35.4, May = 22.5; S. D. for March = 23.50, April = 17.91, May = 15.58; C. V. for March = 5.5, April = 55, May = 69.2.

It has seemed to the writer that for Rhode Island Reds, the zeros formed a wholly artificial class for reasons given in the text; hence, March 1 marks no natural division point in the time at which the birds begin to lay. Consequently, the zero class has been kept separate and not included in calculating these constants. If M includes the zero class, its value for March is 39.8, for April 29.81 and for May 18.1.



while Table V. should also be examined in this connection. It is clear from these graphs that the earlier hatched birds are superior to the later hatched for winter egg production. In the former group there are fewer zero and more very high producers than in the last. There is also a marked difference in the number of birds in each of the several hatching months that laid over thirty eggs during the winter period. (See Table VI.)

The variability in the age at which the first egg is produced influences the winter record strongly, so much so that we have been led to believe that it is the most important determining factor for egg production during the winter months for our flocks.<sup>3</sup> It leads to the abandonment of the view that those records that fall below 30 eggs are made by true mediocre producers, substituting therefor the view that many, perhaps most, of them are late-maturing high producers. Now, the variability in age at first egg, shown in Figs. 1 and 2, is considerable. If this variability could be eliminated—that is, if it were possible to have each individual of a flock of birds hatched April 1, begin to lay on a definite date, say December 1—the birds would make records which would differ from each other in the proportions given by the graphs of rates of production. The fair degree of homogeneity of the flocks in respect to rate of production is shown in part by the coefficient of correlation between the number of days from the first egg laid up to March 1, and the number of eggs produced during that period. The coefficient was found to have a high value, *i. e.*, for 1913-14,  $r = +.8618 \pm .0125$  and for 1915-16,  $r = +.7878 \pm .0128$ . That is, the number of eggs laid is a fairly definite function of the length of the laying period. These coefficients are a rough index of the amount of homogeneity in the flock respecting the rate of production, since a high coefficient implies a fair amount of homogeneity in the flock (*cf.*, however, the statistical constants for rate) for if an egg a day is taken to represent the maximum production while

<sup>3</sup> The results obtained from our breeding tests substantiate this point.



the minimum is represented by a single egg laid during the winter and that one at the beginning of the winter period, no correlation would exist if the scatter is perfect between these extremes. Experience shows, however, that conditions approached by the maximum rate of production are much more common than those represented by the minimum so that the coefficient, even though it has a high value, shows only that the rate of production is comparatively uniform. It does not prove that the flock is composed exclusively of high producers, for, since it is an average figure, the flock may still contain some true mediocre producers. A certain degree of correlation, however, is to be expected in any flock, so that the mere existence of a small positive correlation is of little value, though a low value for the coefficient would imply that there was considerable variability in rate of production. It is quite clear that if a considerable percentage of the flock made records like those shown in Fig. 12, the variability in rate would be much greater than observed, and the coefficient of correlation between length of laying period and number of eggs would be smaller.

*Size.*—Size does not of itself seem to have any specific relation to a bird's ability to lay because birds of all sizes may lay equally well once they have started. It is true, of course, that very large birds rarely make high records, but as there are very few large birds, the chance for a combination between very high egg production, itself uncommon, and large size is rather remote. The converse, however, is not apparently true, for small birds frequently make good records. Since, however, birds that are too small are not desired by poultrymen while as a rule large birds are considered desirable, very small birds are not often trap-nested, so that a strict comparison is at present impossible.

In another way size seems to exert some influence on the record a hen makes. On the average, as shown by the coefficient of correlation between age at first egg and weight, birds of large size reach this size later in life



than small birds do. That is, large size usually, but not always, results from long-continued growth rather than from very rapid growth and as long-continued growth naturally tends to postpone the date at which the first egg is laid, the large hen, other things being equal, can not lay as many eggs. It is possible, however, that the case may actually be the converse, viz., the hen may grow large because she does not lay, though there is no definite evidence for this point of view. While it is easy to find many instances of small birds that mature late in life, instances of large birds maturing at the same age as birds of approximately half their body weight have not been observed. The reason for this is probably to be found in the consideration that while some large birds may grow more rapidly than some small birds, it is always possible for some small birds to grow as fast as it is ever possible for a large bird to grow and hence to mature that much earlier.

*(To be continued)*



## THE CASE OF THE BLUE ANDALUSIAN<sup>1</sup>

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THE blue Andalusian has become the classic in animals as an example of a heterozygote phenotypically intermediate between the parental types. It has also served as an illustration of the failure of dominance for those opponents of Mendelism who consider dominance one of its fundamentals. Furthermore, it has been in constant demand as a classroom example of blended inheritance.

The main facts concerning the breeding behavior of blue Andalusians are, accordingly, more or less familiar. In spite of the long-continued efforts of their breeders they do not come true to color as a breed, but continually throw a certain proportion of off-colored progeny, or "wasters," of two kinds. One is self (entirely) black. The other approaches white, but displays considerable pigment, and is referred to variously as white, splashed, and splashed-white. Since an examination of a large number of birds of this type shows the pigmented feathers to be *blue* in all sections of the female and in those sections of the male which carry blue feathers in the blue Andalusian male, they will be referred to throughout this paper as blue-splashed.

"Splashed" refers to the fact that the pigment does not regularly appear in any particular group of feathers or in any definite region. Feathers located apparently at random on any part of the body may be pigmented over their entire surface or may show only slight traces of pigment. Not infrequently both of these conditions are present in the same individual.

Since the blacks and blue-splashed breed true when

<sup>1</sup> Contribution from the Department of Experimental Breeding, Wisconsin Agricultural Experiment Station, No. 12, and from the Kansas Agricultural Experiment Station.



mated *inter se*, they are considered as being homozygous. If crossed they invariably produce blues.

These facts have led to the current view that the case involves a single allelomorphic pair of characters. The blacks and blue-splashed represent the homozygous conditions, while the self blue is the heterozygote between the two. When blues are interbred, blacks, blues, and blue-splashed are produced in a ratio approximating 1:2:1 for these classes, respectively, which seems to corroborate this view.

Although the blacks and blue-splashed breed true for color, they are not recognized by fanciers as breeds or varieties, and it is doubtful whether they would continue to exist if, much to the disgust of the breeders of blue Andalusians, they did not continue to appear as "wasters" among the progeny of blues. The blues, on the other hand, are quite widely bred. They are officially recognized by the American Poultry Association as a distinct breed and have their place in the American Standard of Perfection. It is interesting in this connection to note that the numbers of blues they throw on the Mendelian expectation barely gets them into the Standard, since the rules of the Association are that no breed can be officially recognized as such unless a minimum of 50 per cent. of the offspring come reasonably true to type (American Poultry Association, 1910, p. 328, Constitution, Article XI).

The blues are quite uniformly bluish-gray throughout the body, with certain exceptions in the males to be noted later. Emphasis has usually been laid on their distinctness from the black and the blue-splashed birds, but it seems important to note their resemblance to these two classes. In the first place, they are like the blacks in being *self-colored*, that is, all feathers in all parts of the body are pigmented. In the second they resemble the blue-splashed in that the color of the individual pigmented feathers is *blue* rather than black, save in certain sections of the males of both classes, where the feathers showing



pigment are a glossy black, apparently a secondary sexual characteristic. The blue appearance is due to the distribution and arrangement of the pigment granules in the feather structure, as will be described later. The fact that the splashed birds are splashed with blue (with the exception noted above) rather than black is important and appears not to have been noted, or at least not emphasized, by previous writers.

As an example, Punnett (1911, p. 70), in discussing the breeding behavior of the blue Andalusian, says: "It always throws 'wasters' of two kinds, viz., blacks, and whites *splashed with black*" (italics mine). In the material which has come under my observation, consisting of upwards of one hundred birds in the unrelated flocks of the poultry departments of Kansas State Agricultural College and the University of Wisconsin, no individual has been noted in which the pigmented areas were not distinctly bluish-gray, except that those pigmented feathers or parts of feathers appearing in the hackle, back, and saddle of the male were glossy black. These sections, it should be clearly understood, are also glossy black in the blue Andalusian male. There are occasionally flecks or small spots of black, appearing in the blue-gray feathers, and even in the white feathers of the blue-splashed birds. This is also true of the blues and, indeed, is not a rare occurrence in both dominant and recessive white races of other breeds. It does not in the least affect the fact that, in the material so far observed, the white birds have been splashed with bluish-gray rather than black in those sections where the blue Andalusian is also blue. This conclusion is borne out by the results of a microscopic examination.

In an effort to determine the fundamental differences between the three Andalusian phenotypes, a careful study of feathers from numerous individuals of each phenotype was made. A detailed account of the results of the study will be published in a later paper. For present purposes a short account of the most obvious differences will serve.



The pigment in all three phenotypes is black. The differences in appearance are due to the distribution and arrangement of the pigment or to its absence.

The pigment in a black Andalusian feather is in the form of rod-shaped granules, which almost completely fill each cell. They extend to the very tips of both curved and hooked barbules, and into the tiny hooklets given off from the barbs of the latter class. The cell boundaries are usually visible, due, apparently, to a slight contraction of the pigment, leaving very narrow pigment-free spaces between the cells. The former position of the nucleus of each cell is almost always plainly visible, due to an accumulation of pigment at its border, and to a narrow area surrounding it that bears relatively little pigment. In appearance, size and distribution the pigment granules in feathers from the black Langshan seem to be identical with those of black Andalusians.

The feathers from blue Andalusians differ from those of the blacks in two important particulars, namely, the restriction of the pigment in the feather structure and the shape of the granules. In blues of average shade, pigment fails to appear in the extremities of the barbules of both types. The hooklets are also entirely pigment-free. Though not always the case, the curved barbules usually carry rather more pigment than the hooked barbules, since the pigment extends further toward the distal end. As a usual thing that part of the hooked barbule which bears the hooks is free from pigment and does not differ in appearance, by transmitted light, from the same portion of a similar barbule from a white feather.

In the pigmented portions the pigment is usually markedly contracted or clumped within each cell, leaving a pigmentless space about the border much wider than is the case with blacks. These spaces are not always clean cut, but may be broken by invading rows of granules, or isolated granules may be found scattered within them. As a usual thing the nuclear boundaries in the cells of blue-gray feathers can only be made out with difficulty, if at all.



In cross-section, the pigment granules are seen to be scattered through the cortex of the barb and along the boundaries of the medullary cells. They are not restricted to the apex of the barb, as is reported by Lloyd-Jones (1915, p. 472, Figs. 37-39) in the so-called blue pigeon.

The predominating shape of the pigment granules in feathers from blue Andalusians is round. There may be a few elliptical granules and occasionally one which can not be classified otherwise than as a rod. These are quite rare, however, and one may carefully scrutinize several blue-gray feathers without finding any but round or very slightly elliptical granules. These round granules quite frequently appear in straight rows, giving the effect of a string of beads.

While the granule shape may have an appreciable effect in giving the bluish-gray cast found in blues and blue-splashed, it seems more likely that, as suggested above, the bluish appearance is due to the restriction or arrangement of the pigment. While the condition is not precisely the same as in pigeons, as described by Cole (1914, pp. 324-325) and Lloyd-Jones (1915, pp. 472-473), the optical effect appears to be from essentially the same causes, namely, the clumping of the pigment within the cells, and the reflection from this pigment through more or less transparent layers of keratin. It appears, however, that in the blue Andalusian the contrast between the pigment-free ends of the barbules and the pigmented barbs and barbule-bases is of more importance in producing the bluish effect than is suggested for the pigeon by these writers.

A characteristic of the typical blue Andalusian not before mentioned is that the contour feathers on the female and the breast feathers on the male present a laced appearance. This results from a black edging on that portion of each feather which is exposed when in its natural position. In this part of the feather the barbules on both sides of the barb are alike, being without hooks. The



cells in these barbules are more heavily pigmented than is true of the rest of the feather and the granules are rod shaped. In the regions where the black is giving way to blue, both round and rod-shaped granules are found.

All pigmented feathers secured from several blue-splashed females show identically the same pigment arrangement and granule shape as predominates in the blues. This holds true whether the portion examined comes from a feather that is pigmented throughout, or from one that is almost wholly white, with but a trace of pigment showing. In feathers which are pigmented throughout, the same relation regarding the lacing occurs as in homologous feathers in blue females.

The statements of the foregoing paragraph apply equally well to the feathers of those sections of the blue-splashed male which are blue in the blue male.

As previously mentioned, in both blue-splashed and blues, as well as in other self-colored races, black flecking or spotting not infrequently appears. Such spots, whether taken from a blue feather from a blue individual, or from a blue or an almost white feather from a blue-splashed bird, invariably show rod-shaped granules, while the surrounding area, if blue-gray, shows round granules. These spots are apparently entirely independent of the factors and conditions discussed in this paper and their appearance is comparatively limited. If hereditary, they probably depend on other factors. In handling blues and blue-splashed, however, one can not help being impressed with the possibility that these spots are caused by some interference with the full expression of the factors responsible for the arrangement and rounding of the pigment granules. Whether this interference is hereditary or environmental is as yet undetermined.

One further fact concerning the blue Andalusian males, already alluded to, is of interest. The long feathers of the neck (hackle) and saddle are glossy black. This is apparently a secondary sexual characteristic, though it is as yet undetermined whether it is due to the presence of



testicular secretion or the absence of ovarian secretion. The black feathers from both sections show rod-shaped granules predominating. There are numerous elliptical granules and a few round granules present. The pigment is not restricted as to distribution in the feather structure and is found even in the tiny hooklets of the hooked barbules, being in all these respects similar to the analogous feathers on a black male. These same conditions prevail in homologous pigmented feathers in a blue-splashed male.

The foregoing describes the conditions that usually prevail. There is some variation in all conditions described. In pure-bred blue Andalusians, for instance, there frequently appear areas that are not the usual clear blue-gray, but are dull and smoky. In such regions both round and rod-shaped granules are found in about equal numbers.

Bateson and Punnett (1906, p. 20) make note of the fact that the adult color of Andalusians may be determined from the down color of the young chicks. Examinations of the down show the same differences in granule shape that are observed in the adults. The blue and blue-splashed chicks for the most part show nothing but round granules in the down, while the blacks show rods.

It is of interest to note in this connection that a section from that portion of a barred Plymouth Rock feather where the black bar is giving way to the white, and the color is dull gray or dun with no bluish cast, there is a dilution of pigment as to amount, but no restriction as to arrangement or distribution. The pigment is fully extended through the barbule cells and consists of rod-shaped granules. There simply appears to be less pigment. While this is the usual condition, here, too, there is variation. At least one barred Rock individual was found whose feathers showed numerous round granules, though the rods predominated.

While it is generally accepted that blue Andalusians, when mated *inter se*, produce blacks, blues and blue-splashed in the ratio of 1 black to 2 blues to 1 blue-



splashed, exact data on this mating, as well as on the back crosses to black and blue-splashed, are really very meager. Bateson and Saunders (1902, p. 131) first suggested that the blue Andalusian was probably a heterozygote. Bateson and Punnett (1905, p. 118) quoted Mrs. Blacket Gill, a fancier of blue Andalusians, to the effect that blues mated to blues gave 22 blacks, 36 blues and 17 white-splashed (*i. e.*, blue-splashed). They secured stock from Mrs. Gill and made matings which gave the following results:

By the blue ♂ the white ♀ gave 34 blue, 20 white-splashed, and the black ♀ gave 27 blue, 19 black. In each case the result is qualitatively what would be expected if the blue is a heterozygote of *black* × *splashed white* [italics mine]; but whether the departure from equality indicates that some gametes bear the unsegregated blue, or may merely be taken as individual irregularities, can not yet be stated.

The same blue cock was bred with a black hen from Experiment 40 (in which the dark birds were unexpected), F<sub>2</sub>, from White Wyandotte × Wh. Legh., giving as offspring 10 black, 15 slaty black to bluish. Hence, therefore, it is evident that the black ♀ was a homozygous black. The 10 blacks are the result of the union of the black gametes from the Andalusian ♂ with those of the ♀, and the 15 slaty resulted from the meeting of the black of the hen with the white-splashed from the Andalusian.

Bateson and Punnett (1906, p. 20) give the following summary of the data upon which the case of the blue Andalusian largely rests at the present time.

In Report I it was suggested that the blue colour of the Andalusian is probably heterozygous, and in Report II (p. 118) figures were given in support of this view. During the past two years additional evidence has been acquired, and every form of mating has now been tested, with the following results:

No. of Experiment	Nature of Mating	Result		
		Black	Blue	Wh. Spl.
Rep. II, p. 118.....	Blue ♀'s × blue ♂.....	22	36	17
Exp. 276.....	Blue ♀'s × blue ♂.....	19	42	22
(Total numbers for blue and blue.....		41	78	39)
[Expectation (inserted by the writer).....		39.5	79	39.5]
Rep. II, p. 118.....	Wh. spl. ♀ × blue ♂.....	—	34	20
" " ".....	Black ♀ × blue ♂.....	19	27	—
Exp. 269.....	Wh. spl. ♀'s × wh. spl. ♂.....	—	—	40
" 270.....	Black ♀ × wh. spl. ♂.....	—	20	—
" 294.....	Black ♀ × black ♂.....	25	—	—



The colour of most of the chickens was determined in the down. In the blacks the down is black with the exception of the ventral surface, the tips of the wings, and sometimes parts of the head, which are white. The down in the blues is slaty-blue, similarly marked with white, whilst in the white splashed it is of an exceedingly pale blue tint as a rule, though sometimes practically colourless.

The above figures bear out the view we previously expressed as to the heterozygous nature of the blues, . . .

The only other definite figures that have come under the writer's notice are from W. J. Coates, a blue Andalusian breeder of East Calais, Vermont, quoted by Platt (1916, p. 665) and referred to by Pearl (1917, p. 149). These are for matings of blue to blue and are as follows:

Mating	White (Blue-Splashed)	Blue	Black	Dark Red
A.....	4	10	3	1
B.....	4	5	2	0
C.....	3	3	0	3
D.....	0	12	1	0
E.....	3	3	1	0
	14	33	7	4

The fact that birds showing dark red appear is unusual and would seem to indicate that the Coates stock differs in its genetic constitution from the majority of the members of the breed, unless the occasional appearance of red is a fact usually suppressed by breeders.

Bateson and his co-workers make no attempt beyond that quoted above to account for the hereditary behavior of Andalusians and appear content to rest the case on the assumption that "blue is a heterozygote of black  $\times$  splashed white."

The fact that "blue" is not a true intermediate between black and blue-splashed does not seem to have received due consideration. While the blue-gray bird is in a sense intermediate between self black and an individual that approaches white more or less closely, this intermediacy is more apparent than real. As previously pointed out, it is not intermediate in regard to either of the conditions involved when they are considered sepa-



rately. It resembles the black phenotype in being self-colored and the blue-splashed phenotype in having the pigment restriction within the barbules, which gives the blue-gray effect.

The 1:2:1 ratio may therefore be analyzed as follows:

Phenotypes .....	Pigment not re- stricted in bar- bule cells; ex- tended through plumage ("self", condition); phe- notype black.	Pigment re- stricted in bar- bule cells; ex- tended through plumage (self); phenotype blue.	Pigment re- stricted in bar- bule cells; not ex- tended through plumage; pheno- type blue- splashed.
Ratio of pheno- types .....	1	2	1
Ratio for restric- tion in barbules	1	3	
Ratio for exten- sion in plum- age .....	3		1

In reality, then, the 1:2:1 ratio is the result of the combination of two 3:1 ratios.

The foregoing facts appear to lend themselves equally well to two interpretations. The first is that there are two pairs of allelomorphic factors at work. The second, that there is one pair of true allelomorphs (*i. e.*, factors having identical loci on homologous chromosomes), neither of which is recessive to the other in its manifestation in the phenotype.

The suggestion of two pairs of allelomorphic factors to explain the case of the Andalusian is not a new one. Goldschmidt (1913, p. 274) makes such a suggestion. After pointing out that the offspring of a pair of blues are black, blue, and "*schmutzigweiss*" in the ratio of 1:2:1, and that all three phenotypes carry pigment, he proposed two factors to account for the condition. The one is an "*Entfaltungsfaktor*," which brings about a full development of the pigment. He represents this factor by "*Q*" (*Quantität*) which is possessed by the black race. The other factor, which is possessed by the "*Weisse*" race, he calls a "*Mosaikfaktor*," which finely divides the pigment. This factor he designates *M* (*Mosaik*). He



finds it necessary to postulate further that  $Q$  is closely linked with  $m$ , and  $M$  is closely linked with  $q$ . Assuming pigment ( $P$ ) to be present in all cases, he represents the "black" gamete as ( $mPQ$ ), the "white" gamete as ( $MPq$ ), and the  $F_1$  blues as ( $mPQ$ )( $MPq$ ). The blue results from bringing  $M$  and  $Q$  into the same zygote. The monohybrid ratio results when the blues are inbred, however, because of the close coupling of the factors within the parentheses.

The Hagedoorns (1914, p. 179) also make use of two coupled factors in accounting for the hereditary behavior of blue Andalusians. They state:

A blue Andalusian fowl, when mated by us to "recessive" white hens did not produce as many blue as white chicks, as should result on the hypothesis, that the white Andalusian is a recessive white (blue and black Andalusians being heterozygotes and homozygotes for one single genetic factor), but exclusively blacks and blues in equal proportions.

To account for this result they propose a gene  $A$  which is present in black Andalusians, but absent in the "white" Andalusian. The blacks, conversely, lack a gene  $B$  which is present in the "whites."

This factor  $B$ , present in a pigmented fowl, actively "dilutes" the colour. It has no effect in the white Andalusians, because these, as they lack  $A$ , are *not pigmented* [italics mine]. We should therefore expect dilute black (blue) young from the cross black  $\times$  white, which, inter se, would give  $AB$ ,  $Ab$ ,  $aB$  and  $ab$  offspring. Now, there is no evidence that in *Andalusians* there are ever produced  $aabb$  animals, or  $AABB$ . There seems to be a mutual repulsion between  $A$  and  $B$ , so that no  $AB$  or  $ab$  gametes are ever produced. In some varieties of fowls this repulsion does not seem to exist, as pure strains of blue chickens occur.

Unless their material differs from any that has come under my observation the Hagedoorns err in assuming that what is frequently termed "the white Andalusian" carries no pigment, and Goldschmidt's suggestion accords more closely with the facts. Further, if the "recessive" white to which they refer was an Andalusian, the production of equal numbers of blues and blacks from a blue  $\times$  white (blue-splashed) cross is difficult to understand. The expectation would be equal numbers of blue-splashed



and blues. If, as I suspect, the "recessive" white was a true recessive from another race, their results can only be interpreted by assuming that the "white" gametes as well as "black" gametes produced by the blue fowl carried a factor necessary for pigment production, which was lacking in the recessive whites.

If the latter is the case it accords with results I have obtained the past season. Among several matings made, preliminary to a further study of Andalusian blue, a white Wyandotte ♂ (*R* 840 from the University of Wisconsin flock) was mated with blue-splashed Andalusian ♀♀ *M* 409 and *M* 539 (also kindly furnished by the poultry department of the University of Wisconsin). From *M* 409 seven chicks were hatched, all of which were unmistakably bluish-gray. Six chicks which failed to hatch, but which did develop far enough for the color of the down to be determined, were also all blues. From *M* 539, brought in late in the season with the hope of increasing the numbers of chicks from this type of mating, three chicks were secured, which were again all bluish-gray. On the assumption that Wyandotte white is recessive (I am surprised to find no statement to this effect in the literature) these results would seem to indicate that a factor necessary for pigment formation as well as one causing the characteristic arrangement or restriction of the pigment found in blues, and both lacking in the Wyandotte, were furnished by the blue-splashed Andalusian. And further that a factor for the extension of this pigment to all feathers on the body was furnished by the Wyandotte. The blue offspring from this mating are assuredly not intermediates between a pure white parent and one that appears to be nearly white.

It is significant to note in this connection that the blue-gray offspring of the white Wyandotte × blue-splashed Andalusian cross show pigment granules that are predominately round. In some individuals they all appear to be round, while in others some rods may be made out. The down of black chicks, offspring of a blue Anda-



lusian ♂ and a white Plymouth Rock ♀, showed only rod-shaped granules. Feathers from a blue-gray individual, whose dam was a blue-splashed Andalusian and whose sire was a crossbred, the offspring of a Houdan ♂ × single-combed white Leghorn ♀ cross, showed only round granules.

If, as Goldschmidt assumes, his factors  $mQ$  and  $Mq$  are so closely linked that they never separate, and behave only as a single pair of factors, it is simpler to assume that there is but one pair of factors. As already pointed out, however, the discontinuity in the gradations from blue-splashed to black is such as to lead one strongly to suspect that two pairs of factors are at work. This discontinuity is greatly emphasized in the case of the blue offspring from the white Wyandotte × blue-splashed Andalusian cross. It is perhaps not impossible that a single pair of factors should bring about the result found in Andalusians, but it is so unusual as to make the assumption of two pairs of factors reasonable.

If this assumption is correct it must be further assumed, as Goldschmidt implies but does not state, that the black and splashed races each contribute a dominant and a recessive factor, and that in the blues we have the expression of both dominants, namely, the extension of pigment to all feathers, furnished by the black (or, in the Wyandotte cross noted above, by the white) parent, and the restriction of the pigment in the feather structure in such a way that the effect is bluish-gray, furnished by the blue-splashed parent. It is of interest in this connection to note that the blue condition produced by the restriction of the pigment in the barbule cells is recessive in pigeons (Cole, 1914, p. 325), while in Andalusians, on the above assumption, it is dominant.

While exact data concerning the breeding behavior of blue Andalusians are exceedingly meager, the experience of breeders generally seems to be in accord with such data as there are, and with the interpretation offered by Bateson and his associates. In order to account for the fail-







$F_2$  1  $Er Er$  = black + 2  $Er eR$  = blue + 1  $eR eR$  = blue-splashed.

The gametes produced by the  $F_1$  (blues) are  $Er$  and  $eR$ . If crossing-over should occur there would be occasional  $ER$  and  $er$  gametes produced. It is highly interesting to note that if these two classes of cross-over gametes were produced in equal numbers, as would be expected, and the individuals producing them were mated with ordinary blues, exactly the same phenotypic ratio would result as from the unions of the non-cross-over gametes, viz.:

$F_1$  crossover gametes  
 $ER, er$

Ordinary gametes of  $F_1$  blue  
 $Er, eR$

$F_2$   $ER Er$  = blue,  $ER eR$  = blue,  $er Er$  = black,  $er eR$  = blue-splashed.

This is the usual ratio of 1 black to 2 blues to 1 blue-splashed and would, from the very nature of the case, escape observation as involving crossing-over unless careful analysis were made of the hereditary constitution of these particular  $F_2$  individuals.

Such analyses would not be impossible, though they might be long and tedious. The matings which would uncover any of the cross-over types, if offspring were produced in sufficient numbers to make it fairly certain that one were not dealing with chance variations in the ratios, are given herewith.

Cross-over blue of  $ER Er$  constitution mated with an ordinary blue would give the following expectation:

$ER Er$  = blue cross-over  $\times$   $Er eR$  = ordinary blue;

$F_1$   $ER Er$  = blue,  
 $ER eR$  = blue,  
 $Er Er$  = black,  
 $Er eR$  = blue,

or 3 blues to 1 black, while the ordinary blues would give the normal 1 black to 2 blues to 1 blue-splashed.

Similarly this same individual mated with ordinary blue-splashed would produce all blues instead of the ordinary expectation of 1 blue to 1 blue-splashed, viz.:



$ER Er = \text{blue cross-over} \times eR eR = \text{ordinary splashed};$

$F_1$                        $ER eR = \text{blue},$   
                               $Er eR = \text{blue}.$

If blue cross-over of the type  $ER eR$  were mated with ordinary black the expectation would be all blues instead of the usual blues and blacks in equal numbers, viz.:

$ER eR = \text{blue cross-over} \times Er Er = \text{black};$

$F_1$                        $ER Er = \text{blue},$   
                               $eR Er = \text{blue}.$

This second type of blue cross-over individual,  $ER eR$ , mated with ordinary blue, would give an expectation of 3 blues to 1 blue-splashed instead of the ordinary 1:2:1 ratio, viz.:

$ER eR = \text{blue cross-over} \times Er eR = \text{ordinary blue};$

$F_1$                        $ER Er = \text{blue},$   
                               $ER eR = \text{blue},$   
                               $eR Er = \text{blue},$   
                               $eR eR = \text{blue-splashed}.$

If black cross-over  $Er er$  were mated with ordinary blue the expectation would be 2 blacks to 1 blue to 1 blue-splashed instead of the ordinary ratio of equal numbers of blues and blacks, viz.:

$Er er = \text{black cross-over} \times Er eR = \text{ordinary blue};$

$F_1$                        $Er Er = \text{black},$   
                               $Er eR = \text{blue},$   
                               $er Er = \text{black},$   
                               $er eR = \text{blue-splashed}.$

This same individual  $Er er$  (black cross-over) mated with an ordinary splashed bird would give an expectation of half blues and half blue-splashed instead of all blues, as in the case of ordinary black and blue-splashed, viz.:

$Er er = \text{black cross-over} \times eR eR = \text{ordinary blue-splashed};$

$F_1$                        $Er eR = \text{blue},$   
                               $er eR = \text{blue-splashed}.$



Finally, blue-splashed cross-over  $eR\ er$  mated with ordinary blue would give an expectation of 1 black to 1 blue to 2 blue-splashed instead of the ordinary expectation of equal numbers of blues and blue-splashed, viz.:

$eR\ er$  = blue-splashed cross-over  $\times$   $Er\ eR$  = ordinary blue;

$F_1$                      $eR\ Er$  = blue,  
                           $eR\ eR$  = blue-splashed,  
                           $er\ Er$  = black,  
                           $er\ eR$  = blue-splashed.

The possible matings not indicated in the foregoing are those which would produce the same phenotypic ratios as if ordinary individuals (*i. e.*, non-cross-overs) of the same appearance as the cross-overs were used. Such matings are naturally of no value for analysis.

If it should later be shown that crossing-over does occur as suggested above and there are two pairs of factors concerned, there is the possibility of occasionally securing  $ER$  gametes. This in turn would seem to make possible the blue Andalusian breeder's long-time dream of producing blues that "breed true." With the appearance of the double recessive gamete  $er$  another race of Andalusian would apparently become possible, which, if the factors assumed in this paper are correct, should be white splashed with *black* instead of with blue.

The second possible interpretation of the facts so far established is that my postulated factors  $R$  and  $E$  occupy identical loci on homologous chromosomes, neither being recessive to the other in its phenotypic expression. For the present at least any evidence that this is the correct interpretation will be largely negative and come from continued failure to find cross-over individuals with regard to  $R$  and  $E$ . If these cross-overs should not be found it might at first appear that the interpretation of the case of the blue Andalusian is in all probability exactly what has been suggested from the first, namely, that blue is a heterozygote intermediate between the parental types.



Such an interpretation makes the characters *black* and *blue-splashed* the allelomorphs.

The practise of referring to *characters* that seem to behave in an alternative relationship in heredity as allelomorphs, instead of *factors occupying identical loci on homologous chromosomes*, is, it is to be hoped, passing. That it has lead to a misinterpretation in the present case is shown by the fact that all the offspring of certain pure white birds mated with blue-splashed ones are blue. The *E* factor must have come from an individual that was homozygous for it and devoid of pigment. It appears reasonable to expect that among the  $F_2$ 's from the white Wyandotte  $\times$  blue-splashed Andalusian cross will appear pure whites that carry the *R* factor. If this proves to be the case the allelomorphs are two factors, *R* and *E*, which act on black pigment. *R* arranges and restricts the pigment in the feather structure so that it gives a bluish-gray appearance. *E* extends any black pigment present to all the feathers of the body. One and probably either or both may be present without any phenotypic expression whatsoever. In fact, for every sixteen  $F_2$  individuals from this cross four pure whites are to be expected in which the genotypic ratio with regard to *R* and *E* is 1:2:1, exactly as in the  $F_2$ 's from a cross of a black and a blue-splashed Andalusian. One of these whites will be homozygous for *R* like the blue-splashed Andalusian. One will be homozygous for *E* like the black Andalusian. And two will be heterozygous for *E* and *R*, as are the blue Andalusians. But because there is no black pigment present these differences in the genotype do not affect the phenotype. For the sake of clearness the expectation of this cross is shown herewith, carried through the  $F_2$  generation. *P* is taken to represent a factor necessary for the formation of pigment which is present in the blue-splashed Andalusian, but absent in the white Wyandotte, while *E* and *R* are represented as allelomorphic to each other.



White Wyandotte ♂ × blue-splashed Andalusian ♀.

	<i>ppEE</i>	<i>PPRR</i>		
F <sub>1</sub>		<i>PpRE</i> = all blue;		
F <sub>2</sub>	6 blues:	3 blue-splashed:	3 black:	4 white.
	2 <i>PPRE</i>	1 <i>PPRR</i>	1 <i>PPEE</i>	1 <i>ppRR</i>
	4 <i>PpRE</i>	2 <i>PpRR</i>	2 <i>PpEE</i>	2 <i>ppRE</i>
				1 <i>ppEE</i>

This same ratio (6:3:3:4), which is to be expected on either interpretation, has been reported by Baur (1914, p. 95) for crosses between a white-flowered race and certain plants bearing ivory-colored flowers, of the snapdragon (*Antirrhinum majus*).

Recessive mutations are of comparatively frequent occurrence. Dominant mutations, though much less frequent, have been described so often that they can not be reasonably doubted. There appears to be no reason, *a priori*, why a mutation might not occur where the mutated factors' potency of expression in the phenotype is approximately equal to that of the normal factor. That this has occurred, not once, but several times, might be the interpretation placed on the striking allelomorphic series reported by Nabours (1914, p. 141) for the color patterns of the grouse locust (*Paratettix*).

Upon which of the two alternative interpretations is correct appears to depend the possible success or the futility of the search for true breeding blues. The first makes it possible. The second appears to close the door of hope in the Andalusian breeder's face unless hope is seen in the progressive selection of the darker blue-splashed individuals. It does not appear possible, on the basis of present known facts, to reach a conclusion. Extensive matings are being made for the coming breeding season which it is hoped will throw further light on the matter.

#### SUMMARY

1. This paper shows that blue Andalusians are like black Andalusians in that they are self-colored. They



are like the blue-splashed in that homologous pigmented feathers in both sexes have the same condition with reference to the restriction of pigment in the feather structure.

2. The fundamental phenotypic differences between black, blue and blue-splashed Andalusians are briefly described.

3. It is pointed out that the 1:2:1 ratio is in reality a combination of two 3:1 ratios.

4. The condition in the blues is shown to be due to the combined action of two factors *R* and *E*. *R* acts on black pigment, restricting its distribution in such a way that it gives the characteristic blue-gray appearance. *E* extends black pigment to every feather on the fowl's body.

5. It is impossible to decide on the basis of present facts whether *R* and *E* are located on identical loci of homologous chromosomes or are the dominants of two pairs of factors, each linked to the recessive allelomorph of the other.

6. It is shown that if the latter is the condition, crossing-over might occasionally occur between *R* and *E* with small likelihood of detection.<sup>2</sup> If crossing-over does occur, *RE* gametes are possible, which appears in turn to make possible true-breeding blues.

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<sup>2</sup>In ordinary practice poultry breeders make what are known as "pen matings," that is, one male is mated to a number of females and the offspring from these females are not kept separate. The exact parentage of any individual is therefore known only with regard to its sire, since its dam might be any one of the females in the group. As the detection of crossing-over depends upon the results of individual matings, it would be practically impossible to discover it under these conditions.



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## THE RÔLE OF FACTOR MUTATIONS IN EVOLUTION

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THE essential features of the mutation theory of evolution, as proposed by de Vries in 1901, are discontinuity and heritability of those variations which make evolution possible. New forms arise from preexisting forms by saltation; they occur in all directions; they are heritable; some of them are advantageous to the species and these are preserved by natural selection. These features are still recognized as the definitive elements of the mutation theory, but biologists are gradually changing their point of view concerning the *real nature of mutations themselves*. De Vries had worked with entire plants as units. He was searching for evidence of species in the making. He believed he had found this evidence when he discovered his new evening primroses at Hilversum and found that they transmitted their divergent characters to their progeny. The evidence appeared none the less clear to him, even though the parent species when tested did *not* always breed true, but continued to produce not only the forms first discovered, but also new ones which did not exist in the original population.

It is not my purpose to discuss the *Oenothera* data which have accumulated in such enormous bulk in recent years. Goodspeed and Clausen, in their papers on species hybrids and the reaction-system concept of Mendelian heredity, have provided a strong argument for attributing many of the so-called mutations among the evening primroses to antecedent hybridization between distinct species. These authors have shown that "the occurrence of the 'mutants' (in *Oenothera*) and their subsequent behavior in hybridization admit of logical arrangement and inter-



pretation without any necessity for assumption of extensive germinal changes." On the other hand, Muller's recent investigation of balanced lethal factors in *Drosophila* led him to conclude "that some (if not most) of the so-called mutations in *O. lamarckiana* are but the emergence into a state of homozygosis, through crossing over, of recessive factors constantly present in the heterozygous stock." If this is correct and these recessive characters arose as factor mutations, it is obvious that, in basing his theory of speciation by mutation on the evidence from *Oenothera*, de Vries builded better than he knew!

During the decade following de Vries's announcement of his theory biological interest shifted from the general problem of evolution to the more specific problem of heredity. The rediscovery of Mendel's law at once focused attention upon the inheritance of particular characters. Then began the era of experimental evolution in which, under the leadership of Morgan, most remarkable progress has already been made. The traditional problem of heredity, its mechanism, has been solved. We know, not only that the ultimate hereditary units are germinal, but also that they are located in that particular portion of the germ cell called the chromatin, and there is an ever-growing body of evidence proving that each hereditary unit occupies a particular locus in a particular chromosome. These hereditary units have been designated by various terms, but are most commonly referred to as genes, genetic factors, unit factors or simply factors.

The germ plasm has come to be recognized as an exceedingly complex stereochemic system, and, as Reichert has pointed out, on account of the impressionability and plasticity of such a system the germ plasm must be exceedingly sensitive to changes in internal and external conditions. That factors, however, are relatively stable entities is being clearly evidenced all the time. But occasionally they undergo definite alteration, doubtless as the natural result of some new or peculiar set of internal conditions. These alterations in genetic factors, or factor



mutations we shall call them, have been most thoroughly investigated in the common fruit fly, *Drosophila ampelophila*, in which species Morgan and others have discovered over 150 factor mutations, each of which is inherited in strict conformity with Mendel's laws, when tested in contrast with its normal mate as it exists in the wild type. This has become the classical evidence for the theory of factor mutations. Furthermore, it is now common practise to refer all Mendelizing characters to their hypothetical representatives in the germ cell, the genes or factors; and we speak of a pair of contrasted characters which are inherited according to Mendel's rule for the monohybrid as due to a single factor difference.

It is well known that Mendelizing characters exist generally throughout all groups of sexually reproduced organisms. Therefore it appears that factor mutations are of general occurrence. The data on factor differences will undoubtedly continue to increase in volume, and as they do our knowledge concerning the relative frequency of factor mutations will become more precise. In general Mendelian phenomena have been observed mostly in conspicuous characters, but certain minute character differences, such as forked bristles in *Drosophila* and size and shape of starch grains in peas, are inherited in Mendelian fashion. *Factor mutations, therefore, are sufficient to explain the origin of all differences between varieties, and doubtless they provide the necessary point of departure in the origin of new races.* If the new characters thus produced are beneficial or advantageous, then natural selection will cause them to be preserved. Sumner has recently discovered a number of interesting mutations in deer-mice (some as yet unpublished) and has shown that isolation may assist in differentiating local races. The writer is not unmindful of the earlier discussions of Wagner and others, and later of Jordan and others, on isolation as a cause of evolution. Many biologists are still inclined to think of geographical differences as the determinative condition in the production of new species. For



example, Harrison has discovered that certain species of moths, which are natives of different continents, but which resemble each other so closely morphologically as to be sometimes indistinguishable, exhibit extreme physiological differences. These physiological divergencies were indicated by the failure of hybridization between these species to produce offspring which were viable, or, if viable, which were fertile. Harrison concludes that geographical differences play a very important part in the production and accentuation of such physiological divergencies.

The rôle of the environment in the *production* of factor mutations is still an unsolved problem. As Caullery points out, the rôle of external factors in the production of mutations is no longer very clearly or directly apparent. It even appears that factor mutations occur in "all directions" quite independently of those elements of the environmental complex which are outside the organism. This does not mean that factor mutations are not caused. Like any other natural event, they must be dependent upon or conditioned by certain antecedent events, and, *a priori*, there is no reason why such antecedent events should not occur outside the organism. In other words, it is reasonable to suppose that specific elements of the external environment might induce permanent alterations in genetic factors. But, as yet, such a specific relation between the external environment and factor mutations can not be said to have been determined beyond reasonable doubt. On the other hand, migration, isolation and geographical differences along with other elements of the environment play an important rôle in the *selection* of mutations, and must, therefore, be recognized as of fundamental importance in organic evolution. It is conceivable, indeed, that, given the occurrence of factor mutations, the continuous impingement of some definite element in the environmental complex during long periods of time might condition a definite orthogenetic trend in phylogeny, as in the evolution of the elephant and the horse. But



may we safely assume the occurrence of the necessary factor mutations? The fact that such mutations are known in many species and that in *Drosophila* the same mutations have arisen anew in the same loci of homologous chromosomes of different pure strains would certainly indicate that we may. A factor mutation probably involves some sort of change within the group of similar molecules occupying a particular locus in a particular chromosome. Obviously the number and direction of the changes possible in such an entity are limited and the sum of the limits of change in all the loci in the chromosome group of a given species would define the limits of factor mutations for that species. The limits and direction of these mutations must have some bearing and may have intimate bearing upon orthogenetic trend.

Factor mutations produce new morphological and physiological characters such as distinguish the forms, races or varieties of existing species. As they occur generally in animals and plants at the present time, we may safely assume that they have occurred in preexisting organisms more or less frequently, and, therefore, that they have played a definite rôle in evolution. But just how extensive is this rôle? Can we account for the whole process of organic evolution including the origin not only of species, but also of genera, families, orders and phyla upon the basis of factor mutations? To be worthy of serious consideration a theory of evolution must account for the development of the organic world as we know it at present. Can the hypothesis of evolution through factor mutations fulfil this requirement?

It is well known that in many genera some of the species differ in their chromosome number. Do factors play a rôle in determining chromosome number? It is possible that they do. It is conceivable that a factor mutation might arise which would so alter the physico-chemical relations between different parts of the chromosome as to cause the chromosome to break at some point. Yet chromosomes are genetic units of a higher order than



factors, each chromosome containing many factors and in general behaving as a continuous entity. Glaser has recently suggested that while the chemical forces determining the specific structure of individual molecules may be precisely analogous to those which account for the nature of the hexose molecule, for example, yet aggregation into linear series in the case of the chromosomes very likely involves elements not strictly molecular. It seems to be necessary, therefore, to postulate some process by which these major entities become altered in number or recombined in entirely new systems. We are dealing here with phenomena of a different sort for factor mutations, and the latter appear, therefore, to be of slight significance in the origin of species having *unlike* chromosome numbers. Alterations in chromosome number may be brought about either by the unique or irregular behavior of one or more members of a chromosome group or by hybridization between species. Natural hybrids between distinct species of plants are of not infrequent occurrence and, according to Lotsy, species hybrids are known in the following groups of animals: Echinodermata, Vermes, Arthropoda, especially the insects, Mollusca, Amphibia, Aves in which even generic hybrids are known, and among mammals where there are several well-known cases of fertile hybrids. As for unique chromosome behavior, several different types have been discovered and are known to occur *occasionally*. Those which contribute directly to chromosome group evolution are: (a) non-disjunction of homologous chromosomes in the heterotypic or true reduction division, preceding gamete formation; (b) failure or retardation of the reduction division, resulting in chromosome groups of three, four or more times the haploid number of the parent species; (c) fragmentation or loss of one or more chromosomes, resulting in gross changes in the germinal reaction system and hence potentially in new species. The occurrence of the last type has not been proved, but, from his cytological investigations of several species of *Drosophila*, Metz in-



fers that within this group of species there has been a definite evolution of chromosome groups.

The known methods of species formation, therefore, may be described as follows: (1) Factor mutations, causing more or less extensive heritable somatic changes, some of which are adapted to the environment and persist. These, under the influence of natural selection, provide the means for gradual differentiation of groups having the same chromosome numbers. Presumably these groups would be recognized at successive stages in the process as geographical or ecological forms or races, distinct varieties and, ultimately, related species. (2) *Chromosome group alterations*, which produce new and sometimes inconstant forms, but which may also produce true species. (3) *Species crosses*, which are known to give rise to new types, some of them constant, but mostly inconstant forms, all of which are cryptomeres, potentially capable of throwing new combinations of parental characters indefinitely. The possibility should also be noted here that new constant types, having different numbers of chromosomes from the parent species, might originate as species hybrids.

Factor mutations occasionally produce new *dominant* characters. This fact, now fully established by various investigations, is of considerable theoretical significance. It has been a common practise during recent years to explain the origin of recessive characters as due to *verlust* mutations, *i. e.*, mutations due to the "loss" of factors. This conception has been associated with the much used though inadequate "presence and absence" hypothesis, according to which the only relations which can exist with respect to a certain factor depend on its presence or absence from the hereditary material. Difficulties are met when attempts are made to explain the origin of dominant mutations in terms of this hypothesis, for in such cases it is necessary to assume that a factor has been added to the hereditary material. As a result of employing the presence and absence hypothesis in genetic nomen-



clature we have the conception of evolution, recently suggested by Bateson and expanded by C. B. Davenport, which holds that "the foundation of the organic world was laid when a tremendously complex, vital molecule, capable of splitting up into a vast number of kinds of other vital molecules, was evolved," and that the process of evolution may be described as the unpacking of this "original package" by the process of loss of factors or portions of factors. Various lines of evidence indicate that changes in species are the result of some process of factor changes. But those who adopt a physico-chemical conception of factors and factor changes will find it unnecessary to imagine the "primordial amoeba" in which was laid the foundation of the organic world as possessing in some mysteriously generalized condition all the genetic factors that comprise the hereditary complex of the genus *Homo*, since it is not by the "loss" or "fractionation" of factors that hereditary changes have been wrought. A gene does not "drop out" or "split up" into two or more—rather *a gene or factor is altered so that its reactions condition a different somatic end product*. It is not by loss of factors, but by changes in the composition of factors, supplemented by intercrossing, that new races, new varieties, and new species having the same chromosome number, originate.

Definite organization of the "hereditary substance par excellence," the chromatin, probably occurred in certain prototypes of existing organisms, in which the chromatic substance was not differentiated from the remainder of the cell plasm. The recent papers of Minchin on the evolution of the cell and of Troland on the enzyme theory of life show that the most probable early course of evolution was from that unorganized state typical of the Chlamydozoa, which are supposed to consist of free chromatin material, up through advancing degrees of differentiation between the specialized hereditary substance and the remainder of the protoplast. Between this fairly satisfactory conception of the earliest steps in evolution and the ever-



strengthening evidence that factor mutations furnish the means for evolutionary change within existing species, it must be admitted that there is a wide gap which needs to be filled. May we not look to future studies on the phylogeny of the chromosomes to supply this need in some measure? I venture to suggest that more work like that of Metz on the chromosome groups of related species will prove to be an important source of further light on this problem.

We may now consider the rôle of factor mutations in more detail. It is certain that even those species having the same chromosome number differ as a rule in many unit factors. Hence in order to explain the origin of one from the other it is necessary to assume one of three possible methods of procedure.

1. There may have been one or more *factor mutations having manifold somatic effects*. That profound somatic differences such as would distinguish species from one another are sometimes produced by single factor mutations is proved by the results of the crosses between the oak-like walnut and its parent, the California black walnut, which I have described in earlier papers. The mutant form, unlike most so-called monophyllous varieties, differs from its parent in every gross external feature, yet it behaves as a simple recessive in  $F_1$  and  $F_2$ . However, *factor mutations which induce such extensive somatic changes seem to be exceedingly rare*.

2. There may have been *simultaneous mutations in several factors*, thus producing full-fledged an individual of a new species. Objection to this hypothesis is found in the observation that factor mutations always or nearly always occur singly, *i. e.*, a single factor mutation in a given individual at a given time. This observation is mathematically predictable since the probability of the occurrence of two factor mutations in the same individual at the same time, according to the principle of least squares, would be the inverse ratio of the square of the number of typical (unchanged) individuals in the popu-



lation. Thus, for example, if one factor mutation occurs in one individual among say 1,000, then the probability of two factor mutations occurring in the same individual at the same time would be once in 1,000,000 times. Moreover, individuals showing even one factor mutation are comparatively rare. Hence, *it appears extremely doubtful that any species have arisen through simultaneous factor mutations in single individuals.*

3. *Single factor mutations may have occurred in different individuals within a group either simultaneously or successively.* This hypothesis implies that individuals possessing certain mutant characters are capable of maintaining themselves in the wild state, an assumption which is justified by the fact that factor mutations are known which have not impaired vitality and fertility, nor reduced the general adaptability of the organism. Further evidence to support this hypothesis is found in the widespread existence of composite species. Although these heterogeneous groups have been classified as species, they are really aggregates of numerous distinct varieties or subspecies. Indeed, their Mendelian behavior indicates that many advantageous physiological characters, such as earliness or lateness of maturity, resistance to disease, high fecundity or possession of a certain pigment, originate through factor mutations. Such mutations frequently, though not necessarily, involve morphological changes also. In all except strictly autogenous (self-fertilized) species new combinations of mutant characters would occur through intercrossing, thus increasing the chances of beneficial or advantageous results to the species. Populations of such species consist of individuals of heterogeneous germinal constitution, and frequently disadvantageous or even lethal factor mutations persist in heterozygous condition, but soon make their presence manifest when inbreeding or self-fertilization is practised. Autogenous species, on the other hand, are composed of individuals of homogeneous germinal constitution (pure lines) which have arisen through the re-



currence of factor mutations. When in a certain germ cell of such an individual a mutation occurs which will produce a detrimental or lethal effect, the offspring will either die or fail to reproduce as the case may be. Hence pure lines possess no lethal or highly detrimental factors; yet these biotypes may vary between wide limits in their morphological and physiological characters.

There is no necessity whatever for the simultaneous appearance of mutations in order to establish new forms. Only three conditions are necessary in this method of evolution: the existence of species during long periods of time; repeated occurrence of some factor mutations resulting in new characters advantageous to the species; and the transmission of these mutations from generation to generation. All these conditions are known to exist. In fact, the repeated occurrence of the same mutation in the same locus of a particular chromosome has been observed, as well as the occurrence of different factor mutations producing similar somatic variations.

Factor mutations, therefore, provide the means for gradual evolution within species; only a few, to be sure, out of many factor mutations being preserved, but these few being sufficient, with the frequent aid of migration or isolation by geographical barriers, to build up new groups which can be recognized only as distinct species. But these new species, it will be understood, would have the same chromosome numbers as the ones from which they arose. We are, therefore, considering here only one of several methods by which new species originate. Strictly speaking, the only true mutations are factor mutations, as they are the only known germinal variations.

#### CONCLUSION

Factor mutations occur in accordance with the general scheme of the mutation theory as formulated by de Vries. They arise suddenly, they occur in all directions, they are heritable, and some of them are advantageous to the species and are preserved by natural selection. When so



preserved they give rise to new forms or races, and when fostered by man they make possible new horticultural varieties of plants or new breeds of animals. It is probable, as Morgan has shown, that factor mutations alone have furnished the necessary germinal changes to make possible the evolution of the elephant's trunk and similar cases of orthogenetic development which have been discovered by paleontologists. But factor mutations alone are not sufficient, so far as we know, to account for the origin of species of different chromosome numbers, much less for the appearance of phyla and genera. It is to be hoped that light will be shed on these more obscure phases of the general problem of organic evolution through a combination of taxonomic, genetic, cytological and physiological researches. It would seem that the solution must involve the expression of relationships between organic groups in terms of the morphology and physiology of the chromosomes.

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PHYSIOLOGICAL PROBLEMS IN THE LIFE-  
HISTORIES OF ANIMALS WITH PAR-  
TICULAR REFERENCE TO THEIR  
SEASONAL APPEARANCE<sup>1</sup>

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I. INTRODUCTION

THE fact that plants flower, fruits ripen, insects appear and disappear in succession throughout a growing season needs no statement even to the savage huntsman or the city flat dweller. The variations of the usual succession of appearances with peculiar seasons, unusual weather, etc., are general guides to many operations of primitive agriculture and matters of comment by all out of door people. Seasonal succession has long been scientifically investigated (see Alee, '11; Forbes, '16; Harvey, '08; Hough, '64; Johnstone, '08; Shelford, '13). Only recently has careful investigation of it been stimulated by the general interest in modern ecology and economic problems. The importance of a knowledge of delayed germination of seeds to the agriculturist (Crocker, '06) has further stimulated work along a line throwing light on the general subject. The analysis of the physiological causes of the normal succession of biological events in any season calls on many of the laws of biology to formulate merely the outline or even a portion of a life history, as, *e. g.*, the answers to questions such as why potato beetles appear from hibernation at a certain time, and not earlier, and deposit eggs on plants of the genus *Solanum*. Further, as soon as we concern ourselves with the analysis of the causes of the irregularities of appearance in any season, the evident complication of problems is such that one may

<sup>1</sup> Contribution from the Illinois Natural History Survey and from the Zoological Laboratory of the University of Illinois, No. 100.



undertake to discuss them without apology. The practical significance of variations to agriculture is shown by the destruction of the wheat crop in the Southwest by the wheat aphid. This was due to differences in response to weather on the part of the pest as compared with its enemies. The cause of seasonal appearance, or more especially of variations of seasonal appearance, is to be found in the influence of external factors on the initiation and velocity of growth and on fecundity and length of life, in dormancy in various stages in the life histories, and in the adjustment of the innate rhythm to the annual climatic cycle.

## II. THE INFLUENCE OF EXTERNAL CONDITIONS ON TIME OF APPEARANCE AND NUMBER OF INDIVIDUALS

1. *Differences in Initiation and Velocity of Development.*—The problem of initiation of development is one that has attracted much attention of late on account of the importance of an ability to predict the time when various insect pests will emerge from hibernation or will reach a stage of development at which it is necessary to spray, if such treatment is to prove satisfactory.

In this connection attention has been directed to the conditions, particularly of temperature, under which there is no development during periods lying within the bounds of the ordinary life history of the animal in question (Sanderson, '10, Headlee, and Peairs). The limit at which development does not take place, usually called physiological zero or zero of development, is better termed *threshold of development*. Sanderson has discussed various data and theories relative to the effect of temperature on development.

The attention of physiologists has been directed toward the study of the effects of temperature on the rate of metabolism and development. In general the results of such study have been interpreted with reference to Van't Hoff's law relative to the increase of reaction with a rise of temperature of 10 degrees, usually des-



ignated as  $Q_{10}$ .  $Vt$  is the velocity of development at any temperature ( $t$ ), so that  $Q_{10}$  is the quotient of  $\frac{V(t+01)}{Vt}$  and supposedly is a constant. In fact, the  $Q_{10}$  is not a constant for living phenomena, but usually varies from 2 to 3, being greater for the lower temperatures and smaller for the higher ones. Snyder has pointed out in detail that while the temperature coefficient for differences of 10 degrees varies, the variation is not only for physiological actions, but also for many chemical reactions; in both cases the variations are in the same direction. He finds that changes in viscosity with changes in temperature follow the same rule. He holds the hypothesis that even in the simpler physiological actions we have to deal with at least two distinct chemical actions whose fundamental velocities at any given temperature are different.

Recently Krogh ('14) has calculated the  $Q_{10}$  from  $Q_1$ ,  $Q_2$  and the like, at different temperatures for the time from fertilization of the frog's egg to the appearance of the first cleavage plane. He found 53.0 (published as 5.3, which appears to be a error) for the interval between 3 and 5 degrees, 4.1 for the interval 5 to 10 degrees, 2.0 for the interval 15 to 20 degrees. He raises the question as to the value of such a variable "constant." He calls attention to the fact that the velocity curve (the reciprocal of the time-temperature curve) is a straight line within certain limits. This is not the curve for the reciprocal of Van't Hoff's time and temperature formula. The latter law is valuable only as evidence that the life process is a combination of chemical processes. The condition of any environmental factor at which development does not take place, but immediately above which development may be initiated, is called the *threshold of development*. It is evident that there is a threshold of development for most species as regards temperature, moisture, light, oxygen, quantity and quality of food, and probably other factors. The brief state-



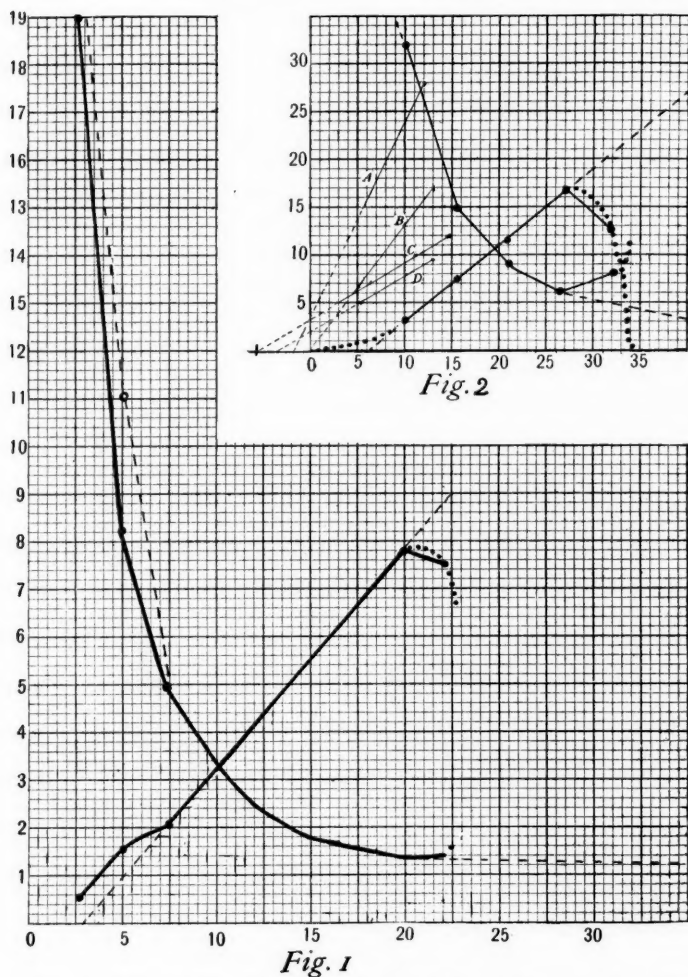


FIG. 1. Showing the time-temperature curve (the longer curve) for the appearance of the first cleavage plane in the egg of the frog. The solid curved line is the actual curve, and the broken line extensions are theoretical, based on the thermal constant ( $\text{time} \times \text{temperature}$ ) where it differs from the actual one. The shorter oblique curve is the velocity curve, or the reciprocal of the time-temperature curve, shown for the true hyperbola by the combined broken and solid lines of the longer curve. It is a straight line. The line of heavy dots shows the probable continuation of the curve based on Verworn's ('99, p. 397) irritability curve. The figures on the axis of abscissas are degrees Centigrade. The figures on the ordinates represent 100 minutes for the hyperbola and 100 divided by the time units for the reciprocal (from data by Krogh).

FIG. 2. Showing the time-temperature and velocity curves for the time from



ments and citations below are in support of this statement.

(a) *Temperature Threshold*

Very nearly at the time of the publication of Krogh's work, Sanderson and Peairs announced that for a large series of insects the time-temperature curve for development is a hyperbola and the velocity of development curve is a straight line. Peairs concluded further that the (reciprocal) relative velocity curve which is obtained by dividing unity (100 to avoid fractions) by the experimentally determined time periods, in days or other units, and plotting it against the temperature for which the time was observed, gives points for the different temperatures which fall in a straight line crossing the axis of temperature at the zero of the curve, or the theoretical threshold of development (Fig. 1). This theoretical threshold may be calculated also with two points accurately determined experimentally. These authors conclude that with the zero determined, the thermal constant (temperature multiplied by time—a constant for an hyperbola) can be obtained. However, they failed to note the deviations from law which occur at both high and low temperatures and which require careful attention in practical work.

These entomological workers appear to have overlooked the work of the fish culturists who have studied the subject of effects of temperature on development. Apstein ('11), Dannevig ('94), Earll ('78), Green ('70), Johansen and Krogh ('14), Reibisch ('02), and Williamson ('08) all made contributions of greater or less importance. All called attention to the effect of tempera-

birth to maturity of *Toxoptera graminum* (from Headlee after Sanderson and Peairs); the velocity curve represented by a heavy line is extended with dots to show the usual form of the irritability curve, and its mathematic extensions are shown as a heavy broken line. The light oblique lines are the velocity curves for the development of the eggs of four species of marine fish (after Krogh). A, the flounder (*Pleuronectes flesus*); B, the whiting (*Gadus merlangus*); C, the cod (*Gadus morrhua*); D, the plaice (*Pleuronectes platessa*). It will be noted that the mathematical zeros of development as indicated are at or below zero Centigrade and the rate of increase in development for each degree of rise of temperature is different for the different species and is indicated by the angle which the velocity curves make with the axes of the curves. The figures on the axis of abscissas represent degrees Centigrade. The figures on the axis of ordinates are days for the hyperbola and 100 divided by days for its reciprocal.



ture on the rate of fish development, particularly during the late embryonic stages. Reibisch ('02) showed that  $\text{time} \times \text{temperature}$  is a constant, using the hyperbola. He called the temperature at which development could be initiated by the slightest increase the "*threshold temperature*," which is the same as the zero of development and physiological zero of other authors. He calculated this from the hyperbola formula, thus anticipating the work of Sanderson and Pears by about eleven years. In fact, the idea of ineffective temperature below a minimum and a sum of temperatures which is the product of  $\text{time} \times \text{temperature}$  dates from de Candolle's 1830 article.

Johansen and Krogh worked over the data of Dannevig and showed that the velocity is different for different fishes (Fig. 2, *A, B, C*). They note further that temperature is not absorbed by the organism and that the constant is only a convenience. They call attention to the fact that the velocity-of-development curve is a straight line which, prolonged downward, crosses the axis of abscissas at a point mathematically corresponding to Reibisch's threshold temperature. The threshold of development would be where the velocity curve crosses the axis of abscissas if the straight-line velocity curve held good and the time-temperature curve were a true hyperbola. Krogh ('14) showed that while 2.7 degrees is the mathematical threshold of development for cleavage of the frog's egg, the first cleavage appeared at this temperature 1,844 minutes after fertilization. If the curve were an hyperbola, at 2.7 degrees the development of the cleavage plane should have required an indefinitely long time; or, in other words, it should not have appeared at all. Also, at 4.9 degrees the appearance of the cleavage plane should have required 1,100 minutes, while the observed time was approximately 730 minutes. Further, it required 138 minutes for the cleavage furrow to appear at 22.1 degrees, which is more than at 20.7 degrees, showing a decrease in velocity at higher temperatures. Thus Krogh points out that the velocity curve is a straight line only between 7



and 21 degrees, while the limit of development is from less than 3 to 22.1.

Thus comparing the velocity curves for Headlee's development of *Toxoptera* (Fig. 1) and for the cleavage of the frog's egg, we note that in the case of the frog's egg the velocity is too great at the lower temperatures and falls off at the highest temperature. Also, in the case of Headlee's curve for *Toxoptera*, the development was much too slow at the higher temperatures. Krogh ('14) further studied the development of pupæ of *Tenebrio molitor*, carefully measuring the carbon dioxide given off. He found that the curve of velocity was a straight line between 18.5 and 28 degrees, but that it curved upward at lower temperatures. He tried incubating the pupæ at 13.45 degrees, which is the mathematical zero of his curve, and found that they developed in 1,116 hours, but with considerable mortality. At approximately 33 degrees the velocity was less than it should be if the curve were a true hyperbola. An interesting feature of these curves is that they approach so nearly to the curve published by Verworn showing the stimulation effect of heat on activity. This curve is shown in Fig. 2 by the actual velocity curve and the dotted extensions which, when compared with the curve of Krogh for the development of *Strongylocentrotus*, *Arbacia*, and *Tenebrio*, indicate the close relation between the amount and rate of activity and that of general metabolism and growth.

Edwards ('02) made a careful study of the hen's egg and established 20-21° C. as the point at which no development takes place. There is an optimum temperature and development is accelerated by slightly higher temperatures and retarded by lower temperatures. Thus even in a warm-blooded species there is a point at and below which development does not occur.

#### (b) Prediction on the Basis of Temperature Laws

Can we predict the time of appearance of any stage in the life cycle of an animal? Certainly, in so far as we



are concerned only with temperature and with temperatures within the straight-line limits of the velocity curve, we can predict with a high degree of accuracy the time at which any stage will be reached. Further, within the

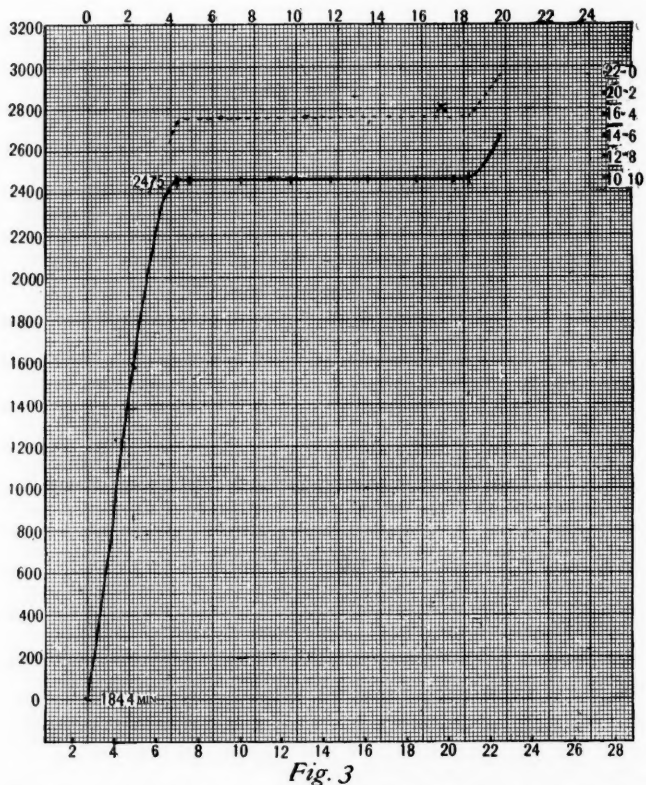


Fig. 3

FIG. 3. Showing the total temperature curve for the appearance of the first cleavage furrow in the egg of the European frog, as a continuous line from the data of Krogh. The small cross dashes show the temperature at which experiments were performed. The actual temperatures are given at the bottom of figure; at the top the actual degrees above the theoretical threshold of development, which is 2.7 degrees C. The figures at the left show the total minute-degrees, time  $\times$  temperature, which range from zero on the scale to 3200. At the right is shown a scale for different degrees of light; these figures are added to illustrate a method of chart-making only. 10 units of light are assumed to give quickest development, and both increases and decreases, to give slower development and hence more time-temperature units, as suggested by the broken line above the main curve. The cross shows approximately what the total time-temperature would be if darkness slowed the formation of the cleavage furrow in the same manner as it slowed general development during an entire month in the experiments of Yung. For further explanation see text.



straight-line limits the effects of constant and variable temperatures should be the same. This is due to the fact that the product of time units  $\times$  temperature above the threshold of development is a constant within the straight line limits. Where it is not a constant, the actual values may be plotted approximately for any temperature.

Using the data of Krogh (Fig. 3), I have drawn an approximate total temperature curve for the development of the first cleavage plane for the egg of the frog. The number of degree-minutes required for completion of the cleavage furrow is the same for all temperatures between  $7^{\circ}$  and  $21^{\circ}$  C. That is time  $\times$  temperature is constant between  $7^{\circ}$  and  $21^{\circ}$  C., where it is about 2,475 time-temperature units or minute-degrees, and the curve is a straight line. Above 21 degrees the total temperature is greater than the constant, and below the lower limit of the constant it is less than the constant. At 2.7 degrees it should be infinity if the hyperbola held good, but is actually 1,844 minutes. The time-temperature units are not expressible at this point, so the actual time is given. If development takes place below the zero of the hyperbola, the time-temperature units may be considered as having a negative value, but are expressible. From this curve it is possible to tell how long it takes for the cleavage furrow to develop at any temperature shown; for example, take 6 degrees (bottom of chart =  $3.3^{\circ}$  degrees at top). We find from the curve that the total temperature for this is approximately 2,200 degree-minutes. Thus, 2,200 divided by  $6.0 - 2.7$  gives 666 minutes. It is true that the same result could be obtained by reading off the time on a time-temperature curve (near to hyperbola) with less labor, but the region in which the total temperature is a constant cannot be shown on such a curve; and the time for different temperatures is obtained with less simple calculations from the reciprocal. The total temperature curve exaggerates the straight-line limits, and brings out sharply the fact that high temperatures retard and low temperatures accelerate as compared with the veloci-



ties indicated by the reciprocal of the hyperbola to which the data partially conform.

Factors other than temperature influence the rate of development. The work of Yung showed that in the case of the frog light is one of these. Unfortunately the light was not measured definitely in the work of either Krogh or Yung. Yung kept one lot of developing frogs in the dark and one in a window but where the sun actually never shone on them. Krogh's work must have been done in similar light. Yung's larvæ were reared under the light conditions which he used, for a month or two months, and thus his data are for older stages than those of Krogh, whose results relate to the appearance of the first cleavage furrow. Accordingly, any comparison of the two sets of data is essentially impossible. However, for the purpose of illustrating a principle which is indicated relative to development under the influence of various intensities of factors other than temperature, I have called the light condition under which Krogh's work was done 10 units and have shown it on a scale at the right-hand side of the graph. It is probable that too strong light will retard development as well as too weak light. Hence the scale is shown double, 12-8, 14-6, etc.; either increases or decreases in light intensity are assumed to increase the time required for development. The cross shown on the graph gives the approximate total temperature for darkness indicated by Yung's work. This part of the chart is given merely to indicate a method of chart making—of showing the way in which variations of one other factor change the number of time-temperature units required for development.

For practical prediction such a curve must be drawn for the shortest time for development at each temperature. This will be under optimum light, chemical, etc., conditions for the temperature concerned. In establishing such a least-total temperature curve a few careful determinations within the straight-line limits with other factors optimum will suffice. Outside these limits the de-



terminations must be more numerous and especial care must be exercised to have the temperatures constant. In determining the optimum light for different temperature much more rapid progress can be made by running experiments under at least three conditions of this factor for each temperature. Deviations due to factors other than temperature should be shown on such a chart probably in a manner indicated by the broken line on Fig. 3. If the main curve is drawn for shortest time, all deviations in light, etc., will *increase* the so-called total temperature, and lines may be drawn for these conditions above the main curve as the facts necessitate.

Much investigation will be necessary to determine the corrections which must be made in determining *mean* temperatures which must be derived from conditions in which the temperature slowly rises and falls during several hours of each day, within the ranges of temperature where the velocity curve is not a straight line. Temperatures outside the straight-line limits should not be mixed with the temperatures of the straight line limits. These outside temperatures must be considered or estimated in terms of units sufficiently small to approach accuracy. In the case of daily temperature fluctuations the temperatures outside the straight-line limits must be considered by hours, and suitable corrections made before they can be included in the daily mean. The exact nature of this correction will have to be determined by careful investigation.

#### (d) *Humidity Threshold*

The workers thus far cited have studied temperature alone, intending in a general way to keep other factors constant. There is undoubtedly a threshold of development with reference to each factor which influences development. Berger found that growth ceased in tenebrionid larvæ fed on bran dried at 105 degrees, and that they lived for months with a loss of weight; doubtless with a very small increase in moisture they could be maintained at the initial weight. More recently Pierce has found



that the cotton boll-weevil has a different zero or threshold of development and different temperature optimum for each humidity.

(e) *Oxygen Threshold*

The development of various invertebrates is stopped by insufficient oxygen (Loeb, '06, and citations). Johansen and Krogh found that if the oxygen pressure was reduced to one half by reducing the air pressure to 380 mm. of mercury development of plaice eggs was retarded. The oxygen pressure threshold of development lies below the amount which will go into solution from air at pressure of 230 mm. of mercury, but at this concentration much care was necessary to keep the eggs alive. Shull ('11) determined the oxygen minimum for the germination of the seeds of *Xanthium*.

(f) *Light Threshold*

Loeb ('11) states further that light is necessary to the regeneration of zoids in *Eudendrium*. Its absence is further known to slow development in larvæ of insects which normally live in the light (Bachmetjew, 692). Smith found that light accelerates the development of salmon. Johansen and Krogh found little difference between marine fishes grown in light or in dark. Davenport ('99) summarized the literature to that date and showed on the authority of Yung that moderately strong light increased growth.

(g) *Food Threshold*

Recent work has shown that food may be either qualitatively or quantitatively deficient and cause standstill in the development of mammals. Thus Osborne and Mendel (p. 101) show the following methods of producing it:

(1) By under-feeding with rations of suitable qualitative make-up; (2) by the use of diets containing an adequate protein but with inorganic salts supplied in the form of a mixture of pure chemicals together with sucrose and starch as the carbohydrate component; (3) by restricting



the protein content of the dietary below the minimum required for growth; (4) by furnishing as the exclusive source of nitrogenous intake proteins which lack some amino-acid group indispensable to growth.

Thus the animals were maintained at practically the same weight and they retained their power to grow long past the age at which growth normally ceases (335 days) and for periods equal to half the normal life of the species, which is 1,000 days.

Wodsdalek ('17) has shown that certain tenebrionid larvæ can not only be maintained, but may be reduced from half-grown to hatching size several times by repeated starving and feeding. This seems to leave little doubt as to the existence of a threshold of development for food.

#### (h) *Definite Amount of Development*

Krogh has shown that the total amount of carbon dioxide given off by pupæ of *Tenebrio molitor* is the same for all temperatures, showing that there is a definite amount of development to be attained. The rate appears to be different for different species where no considerable difference in the total for passing the stage in question is to be expected, as in the case of fishes (see graphs by Krogh). Thus, difference in velocity and increase in velocity at different temperatures and moistures, etc., have an important bearing on the variable or unequal seasonal appearance of the different species. The acceleration of development under conditions of factors near the threshold is a further consideration (for a noteworthy instance see Bachmetjew's ('07) retabulation of Merrifeld's ('90) data) which leads to non-coincident appearance and peculiar modification of normal sequence in abnormal seasons.

It appears that the chief reason that there are not more generations in an annual cycle in the case of spiders or other animals is that the amount of energy which must be expended and the velocity of development are such



that the completed sexually mature individual can not be produced oftener than usually obtains. There is, to be sure, much evidence that the tendency to hibernate is not very firmly established in some species and that under stimulation animals may be induced to reproduce nearly continuously, at least for a number of generations. Cessation of development in any given case is as much attributable to some factor falling below the threshold of development as to heredity. The environment is extremely complex, and the number of factors which may cause cessation of development and which have been already established, are so numerous as to indicate that the number is very much greater than is commonly supposed, including temperature, moisture, light, oxygen, evaporation, quantity of food, or absence of any one of many necessary food constituents. These appear to operate in accordance with the law of toleration (Shelford, '13) and, with respect to food, in accord with Leibig's law of minimum. Where dormant periods are well established, their occurrence with reference to the usual seasonal rhythm makes any modification of the usual life history difficult or impossible.

Variations from the "normal" seasonal weather, and weather changes are of especial interest as modifying the usual seasonal succession of adult animals or any area. In springs with unusually prolonged cool weather, the various pond species, such, for example, as those noted on page 146, are crowded together, and reach maturity much more nearly at the same time than in normal seasons. The same phenomenon has been observed by the writer in the case of the flowering of early spring plants of an area near Chicago. The differences in the response of different species to the same conditions show their different physiological constitutions. This type of variation indicates that such maladjustments as resulted in the depletion of the grain crop by the grain aphid in the southern part of the wheat belt, because the weather favored them, may occur in undisturbed localities, though



probably not to the same degree. Seasonal succession and its variation involve, for the pure-science student, many of the problems which confront the economic zoologist.

3. *Length of Life and Fecundity*.—One phenomenon which has been repeatedly noted in connection with this study—a matter of common observation—is the variation in numbers of individuals in different years. The length of life of individuals may have a pronounced effect on the population and succession of species on a given area. Loeb has stated that the great number of individuals in the plankton of the polar seas in summer is due to the longer life of the individual at low temperature. Unless the low temperature slows the different processes unequally this can hardly follow. For example, if a parthenogenetic female aphid normally lives a week and produces 1,000 offspring and then the temperature is lowered so as to prolong the life to three weeks, unless the different functions were unequally affected by the change, there would be at the end of three weeks but a thousand, while at the normal rate there would have been a billion possible individuals. On the other hand, if the rate of reproduction remains the same and the length of life of the individual after the reproductive period is increased, the results of lower temperature would be very different, perhaps much as Loeb assumes. Actual observations along this line are few. In the case of the San José scale, however, Glenn ('15) found that the number of offspring is greatest in the individuals breeding in the warmest weather. Turning to Table I we note (page 146) that *Agelena nevea* may live longer in the adult stage than *Argiope aurantia*, or the time of appearance may be more irregular, and hence the question is one for investigation.

The velocity of development of different species is different, and the relative velocity is measurable in some terms of the angle which the velocity curve makes with the axis of abscissas (Fig. 2). Thus when we compare the four species of fish given by Dannevig we note that



velocity of development increases more rapidly with increases of temperature for the flounder than for the plaice; the same difference exists between the whiting and the cod. Krogh showed that the velocities of the different stages of the frog's egg, Fig. 1, are the same; but the different stages in the life history of the same animal may differ in velocity at the same temperature.

4. *Dormancy*.—Dormancy is of much importance among animals inhabiting the same area. Thus the eggs of *Eubranchipus* and *Diaptomus staghalis* require both summer drying and winter freezing before they will hatch. Dormancy is common in the eggs of grasshoppers (Thomas, '79), walking sticks (Trouvelot), etc. Dormant periods are common, occurring even in deer and armadillo embryos (Patterson), and probably represent hereditary remnants of impressions made on former generations by seasonal rhythms.

The causes of these rhythms often are simple. Concerning delayed germination or dormancy of seeds, Crocker and Davis ('14) have said:

The work to date has shown that delayed germination of seeds is secured in a variety of ways: by almost absolute exclusion of water by seed coats (as in the hard-seeded legumes and species of several other families), by the limiting of the degree of swelling of the embryo, . . . by reduction of oxygen supply below the minimum for germination . . .; and finally perhaps by deficiency in salts. To this must be added delays due to embryo characters.

Dormancy has been overcome by drying in the case of several species of insects in the writer's laboratory.

### III. SEASONAL SUCCESSION AS ILLUSTRATED BY THE SPIDERS OF A SMALL AREA OF GROUND

In the spring and summer of 1910, Mr. G. D. Allen undertook the study of the seasonal succession of the fauna of an area in a vacant lot at Eighty-first Street and Blackstone Avenue, Chicago, which is a pond in spring and low prairie in summer, but did not complete the work, though his collections were extensive and thorough, extending



from the middle of June to November. Miss Katherine Norcross arranged the records in seasonal order, except those of the spiders. In the case of the insects which made up the vast majority of species on such an area, the question constantly arose as to where the insect had been previous to its appearance there. During the spring and summer of 1913, the writer undertook to collect and observe the spiders of the plot studied by Allen. Spiders were selected for this study because they do not undergo a metamorphosis, and may often be found and identified in a juvenile condition while insects can not. Though incomplete, the data are adequate for a discussion of the physiological features of seasonal succession.

The habitat from which the specimens were collected was about  $25 \times 50$  ft., nearly all of it covered with water in early spring, usually drying during May, and containing water thereafter only during and after especially heavy rains. In July Allen found the vegetation composed chiefly of *Eleocharis*, *Spartina*, *Carex*, *Juncus*, *Liatris*, *Steironema*, *Cacalia*, and several other composites. The plants taken together made up what is commonly called coarse grass and weeds. The writer's collections in 1913 were made on or very near Allen's dates for 1910. From these joint sources the data of the following table were obtained and arranged, but with some gaps where the spiders were probably too young to identify. The records marked "C" are taken from Comstock ('11) and represent the conditions in which the spiders usually are at the dates indicated. The spiders were identified by Banks ('10) and the nomenclature is according to his list.

1. *Statement of Succession*.—In the spring the area is a pond in which various Crustacea and worms succeed each other (see Shelford, '13, pp. 278). Sexually mature adults appeared in abundance about as follows: *Amblystoma tigrinum*, March 15; *Eubbranchipus*, April 15; *Planaria velata*, May 1; *Diaptomus stagnalis*, May 1. Some of these animals have been studied sufficiently to show that they become dormant for the remainder of the year



as soon as the pond dries up. *Amblystoma tigrinum* deposits its eggs and then burrows into the mud and remains ten months in estivation and hibernation. *Eubbranchipus* deposits eggs that must be both dried and frozen before hatching. *Diaptomus stagnalis* is similar in character. *Planaria velata* forms cysts which live over to the following spring.

TABLE I

SHOWING SEASONAL SUCCESSION OF ADULT SPIDERS ON A LOW PRAIRIE SUMMER DRY POND

The species are arranged in the order of the seasonal occurrence of adults. \* indicates adults; j, young; e, eggs; g, generic identification only. C indicates that the occurrence is creditable to Comstock and is not based upon the author's observation. Dates are given at the heads of the columns in numerals only.

	4-20	5-6	5-22	5-26	7-10	7-24	8-6	8-6	9-30	10-12	11-6	Adult Weight in Gg.
	1	2	3	4	5	6	7	8	9	10	11	
<i>Pardosa modica</i> Blek. ....	*	*	*									
<i>Tetragnatha laboriosa</i> Htz. ....	gj	*		*		*j	*	j		j		
<i>Xysticus gulosus</i> Key ....	gj	*	*	*				*	*	j	j	
<i>Dictyna sublata</i> Htz. ....		*				j	j	j	j	j		
<i>Pisaurina undata</i> Htz. ....		*				*j	*j	j	j	j		300
<i>Attus palustris</i> Peck ....		*		*			*					
<i>Pardosa canadensis</i> Blek. ....	gj	j	j	*	*							
<i>Lycosa heluo</i> Wal. ....				*	*			*				
<i>Phidippus podagrosus</i> Htz. ....	j	j	j	*j	*		j	j		j		200
<i>Plectana stellata</i> Htz. ....				*j	*		*		*			25
<i>Epeira trivittata</i> Key ....					*		*	*				
<i>Runcinia aleatoria</i> Htz. ....					j	*	*					160
<i>Mangora gibberosa</i> Htz. ....						*C	*	*				
<i>Agelena nivea</i> Wal. ....			jC	j	j	*	*	*	*	*	eC	80
<i>Misumessus asperatus</i> Htz. ....				j	j	j	*j					
<i>Phidippus audax</i> Htz. ....	jC	jC	jC	jC	jC	jC	*	*j	*jC	jC	jC	80
<i>Argiope aurantia</i> Luc. ....	jC	jC	jC	jC	jC	jC	*	*	*	jC	jC	
<i>Argiope trifasciata</i> Forsk. ....	jC	jC	j	j	j	j	*	*	*	eC	jC	425

At the time these appear, land animals begin to move about the pond margin, adult and juvenile spiders among them. The collection and arrangement of the entire fauna showed the same thing as the spiders, but proved much less satisfactory in the other cases than was expected, owing to a lack of knowledge of life histories and an inability to identify young stages. Turning to Table I and following out the stars which indicate the occur-



rence of adults, and noting that the species have been arranged in the seasonal order, starting with *Pardosa modica* Beck, which was taken only in April, we end the season with adult *Argiope trifasciata*, which appeared as adults late in the season only.

We note that when the collection proved at all complete the juvenile individuals follow the adults of the early spring species, and that they both precede and follow the species which mature late in the season. The collections proved to have been made with insufficient detail, and many young spiders could be identified only to the genus and are usually omitted entirely. However, the tables show a sufficient general arrangement of the species throughout a season to furnish an adequate basis for a discussion of the problems involved in the phenomenon of seasonal succession—the problems presented by a comparison of the few species whose life histories are known quite completely.

#### IV. DISCUSSION

Nearly all species are adjusted to the seasonal rhythm of the habitat in which they live. Thus *Dytina sublata* appears as adult in May and June, when, as it seems, eggs must be laid, and juvenile forms characterize the late summer and autumn. *Argiope trifasciata* deposit eggs in October and passes the winter in the juvenile form. *Phidippus podagrosus* reaches maturity in July, when eggs must be deposited, and young occur in both fall and spring. These differences generally represent an innate adjustment of the life cycle to seasonal rhythm, not readily broken up. It is to be expected, then, that *Dictyna* will deposit eggs to better advantage and that the young hatch better in May than in November, as is the case of *Agelena nivea*. It is further to be expected that the young stages of some spiders will not go on with development until cooled for a considerable period. Perhaps one of the most interesting questions concerning the whole matter of succession of spiders is to be found in the fact that from what is known about them, they are all active



for about the same period of time; *i. e.*, all life histories involve about the same period of activity and rest.

An inspection of the table shows that the time of reaching the adult stage varies for the different species, so that there is a general change of spiders in the adult stage as the season progresses. This is all that seasonal succession can mean under any conditions; the fact that the eggs or other young stages can not be identified or their location is unknown does not change the character of phenomenon in any locality where the species are resident.

The causes of the succession of species may be roughly summarized as follows: Species differ in the time in the annual climatic rhythm at which development begins, in the time of occurrence of dormancy and in the conditions necessary to break it up, in threshold of development relative to several climatic factors, in velocity of development relative to several climatic factors, food, etc., and in size and total energy expended. These may be taken up one at a time.

Considering differences in the time in the annual cycle at which development begins, as a factor in seasonal succession, we must notice first that this can be a controlling factor only where there is no dormancy in the life history or where the available total of temperature, moisture, light, etc., above the thresholds is just enough to produce one generation per year and not to permit of a gradual moving of the time of appearance to an earlier date each season, during several successive long seasons. The test of this would come in the migration of agricultural pests which are arrivals in localities where the growing season is longer. There appear to be no easily available facts, and for the present this type of maintaining a definite time of appearance is to be regarded as a theoretical possibility. The fact that the life histories of various animals which have been known to migrate extensively into new territory appear not to be accelerated indicates that dormancy may control appearance and thus time of beginning development may be a secondary consideration.



Thus we come to the time of occurrence of dormancy and the conditions necessary to break it up, which result in the rhythmic tendency of the species fitting into the rhythm of the climate in which it lives. In many insect species it appears that drying may be substituted for freezing. Such species may migrate into climates in which there is a dry season, instead of a cold one, and with a longer growing season, and continue with the usual annual life-history rhythm. Under these conditions in each growing season the development is stopped by dormancy and proceeds no further until the drying breaks up dormancy. The development of *Eubbranchipus*, once initiated, proceeds until the mature individual has produced eggs. Here dormancy stops all further progress until the eggs are first dried and then frozen and warmed above  $0^{\circ}\text{C}$ . Crustacea without dormant periods go on developing and produce several generations in one summer. After the conditions necessary for the overcoming of the dormancy have been fulfilled, or where there is no dormancy, species differ in the threshold conditions for development. The thresholds for development are hardly the same for any two species in which thresholds have been determined. Thus species will differ in the time at which development is initiated in the spring. Further, the increase in velocity with increase in temperature is different for different species, as indicated by the differences in the angle which their velocity curves make with the axis of abscissas (see Krogh, '14, velocity curves of several species of fish, also Fig. 2). This fact alone makes it possible for a given set of conditions out of the ordinary to give a peculiar and irregular occurrence of the different species of a community.

The total energy as illustrated by the  $\text{CO}_2$  given off by a species is the same for all conditions in which development can occur at all, as shown by Krogh. It is probable, accordingly, that the total energy expended in development is different for each different species. This may bear some relation to size and weight, though alcoholic



specimens of full-grown females of several species of spiders were weighed and no conclusion could be drawn. Either the method of obtaining the data or the fact that the spiders are all annual is the cause. Krogh found that the velocity of development is the same at the same temperature in the different stages of the frog, though the thresholds are different. But there is no reason to assume that this is true of other animals, especially where there is a metamorphosis.

1. *Conclusions.*—The preceding pages indicate the intricacy of the problems involved in explaining the simplest life history of annual animals. The physiological life histories of animals which have two or more generations per year, and of those whose life cycle extends over more than one year, are still more difficult to deal with. The problems involved have of late attracted the interest of biologists generally, of geneticists, of economic entomologists, of fish culturists, and others, and they constitute a central group of problems for the ecologist. All these various interests are being focused on the problems of physiological life histories as the next step in the attempt to advance the science of biology. In all these lines, the day of the naturalist taxonomist as a central figure is all but past, and the day of the naturalist physiologist is at hand.

This interest has arisen in the various groups for different causes, but one of them is the variation which occurs in the succession of species and their interaction in different years, due to peculiar weather conditions. The green bugs destroyed the wheat crop in 1907 because of differences in thresholds of development of the aphid pests and their enemies; the fruit growers do not spray at the right time in many cases because the insect pests do not appear at the usual time. This is not to be credited to the effects of one factor alone; as, for example, enough work with temperature has been done to show that, while it is important, the influence of other factors is sufficient to make prediction on the basis of temperature alone quite unreliable.



The animal geographer is interested in the same problems. We note that the animal community illustrated by the spiders contained animals maturing at every season of the year. There is a noticeable early spring or vernal group which the geographer has assumed is montane in origin (Adams, '09); and the group of land species which appears through the summer is traced into different situations according to specific affinities. It is evident that successful species are those that fit into the seasonal rhythm with respect to physical conditions, food, and numerous other relations.

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## THE USES OF INSECT GALLS

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### INTRODUCTION

THIS paper, which is a contribution from the Branch of Forest Insects, Bureau of Entomology, is a summary of an extensive study of the literature dealing with the uses of insect galls. It was made primarily to obtain a history of the use of the Aleppo gall in the dyeing industry. In the preparation of this paper I have been assisted by Mr. S. A. Rohwer under whose direction the research of the literature was made.

For centuries before the real origin of insect galls was known, they were noted and given a place, like most other vegetable substances, among remedies for diseases. The ignorance of their origin gave rise to queer superstitions and practises even among scholars, especially in the Middle Ages, when they were gravely recorded as supernatural growths and employed as a means of foretelling the events of the coming year. The gall was supposed to contain a maggot, a fly, or a spider, each of which betokened some misfortune. If the inhabitant were a maggot the coming year would bring famine, if a fly, war, or if a spider, pestilence. This belief was recorded and practised for several centuries, even after the time of Malpighi, who was the first in the Western World to discover and make known the true origin of insect galls.

The record of the practical use of galls has come down from the old physicians and naturalists of Greece and Rome. Their observations were confined chiefly to the Aleppo gall and the Bedeguar of the rose, but an interesting statement is found concerning two galls which were used by the Greeks to burn without oil in their lamps.



These were *Cynips theophrastea* and an undetermined gall called by Pliny the black gall-nut.

Until very recently in all histories of drugs, tanning, and dyeing, galls have been considered as of great importance, and at the present time are among the most valued ingredients of ink. The first use of galls was in medicine and many besides those discussed below have been listed as drugs.

Among the Cynipids is the gall of field cirsium produced by *Cynips* species (determined by Cuvier) which was formerly considered, if merely carried in the pocket, as a very efficacious remedy for hemorrhages. Others merely mentioned are (*Cynips quercus-terminalis*) = *Biorhiza pallida*, *Cynips polycera*, *Cynips quercus-toza*, *Dryophanta quercus-folii*, *Andricus fœcundatrix*, and the undetermined galls called by Guibort, *galle corniculée*, *galle marmorine*, and *galle d'Istrie*. This last, according to Trimble, yields 24 per cent. tannic acid.

Besides the Cynipid galls there is a gall on *Pistachia khinjuk*, called Gúl-i-pista, produced by *Pemphigus pallidus*, which enters into the materia medica of India. Two other Indian galls used in medicine are found on *Tamarix*. One, called Bara-Mai, occurs on *Tamarix gallica*, and the other, Chota-Mai, occurs on *Tamarix orientalis*. Another *Tamarix* gall said to have been used by the Egyptians in medicine is one called by them Chersamel, and by the Turks, according to Fockeu, Bazgendge.

To the Cynipids useful in tanning Kieffer has added *Cynips lignicola* and *Cynips hungarica*; and to those used in dyeing, (*Cynips tinctoria-nostra*) = *Cynips infectoria* Hartig. *Cynips quercus-petiole* Linnæus, according to the *Gardeners' Chronicle*, 1854, is also capable of forming a strong black dye.

Burton in his journeys in East Africa noted a gall-nut which was used by the Somali women as the basis of their tattooing dye. This gall has not been determined, but the record is of interest as being the only one encountered of a savage people's making use of galls.



Another undetermined gall is that called by Pomet "Bazdyendge" and described by him as a reddish gall on a species of oak in Turkey, which was used with cochineal and tartar to make a very fine scarlet.

So far as can be ascertained no American galls were ever used for any practical purpose by the Indian (statement of Dr. Hough, U. S. National Museum), and but few by the white man. No interest appears to have been taken in this phase of gall history in America until Trimble, through his interest in the history of tannins, took up the question of tannic acid in galls and analyzed a few North American galls. He found that many of these galls contained relatively large amounts of tannin. He stated that there are more oaks in the United States than in Europe which are available for tanning, and that as the gall partakes of the character of its host-plant then there must necessarily be more oak galls in this country suitable for tanning. He also remarks that it is not known that all species of oak yield the same tannin, therefore we may look for a variation in the properties and composition of the tannins from different species.

Of the Cynipid galls examined by Trimble the richest in tannin is one from Texas, on *Quercus virens*, closely resembling the Aleppo gall and containing 40 per cent. tannic acid. This has been identified by Mr. S. A. Rohwer as *Disholcaspis cinerosa*. *Acraspis erinacei* (determined by L. O. Howard) was found to contain 17.89 per cent. tannic acid and *Disholcaspis globulus* Fitch, 3.91 per cent.

A Dipterous gall on *Quercus alba*, determined by L. O. Howard as *Cecidomyia* or *Diplosis* species, contains, according to Trimble, 9.24 per cent. tannic when air-dried, and 31.68 per cent. when quickly dried by artificial heat at 80 degrees.

A gall occurring on *Rhus glabra*, in many ways the counterpart of the Chinese gall, was found by Trimble to yield, when air-dried, 61.70 per cent. tannic acid which is about 8.3 per cent. less than the Chinese galls yield and about 3 per cent. less than the Aleppo. This has been



identified by Mr. A. C. Baker as *Melaphis rhois* Fitch.

Besides the American galls suggested by Trimble as being of possible use in the industries, a few have been recorded as food.

The galls of *Disholcaspis weldi* (Beutenmüller) which occur on *Quercus reticulata* in Mexico were purchased at a fruit stand in Mexico City.

Oak-apple galls produced by *Cynips* spp. are eaten by school children, and some of them are said to be sweeter than sugar.

The most important record on the use of American galls is a note by Dr. A. D. Hopkins on a black oak gall produced possibly by *Callirhytis* sp. This gall, because of its resemblance to wheat, is called "black oak wheat" and "wheat mass" (typographical error for mast<sup>1</sup>). Specimens of this gall were received from Westcott, Mo., with the information that they were very abundant and had been fed to cattle, hogs, sheep, turkeys and chickens all of which were fond of them and were getting fat on them. These galls were also received from Texarkana, Ark., where they were used to fatten hogs.

The following food analysis and report were made on these galls in the old Dendro-Chemical Laboratory, Bureau of Chemistry, U. S. Department of Agriculture, under the direction of the late Dr. W. H. Krug:

	Per Cent.
Moisture .....	12.24
Ether extract .....	3.37
Crude fiber (indigestible) .....	9.34
Protein .....	8.56
Ash .....	2.89
Carbohydrates (starch, etc.) .....	63.60
Relative food value =	93.43
Nutritive ratio =	8.4

The relative food value is high and the nutritive ratio is wide, showing that this material is especially adapted for fattening animals.

<sup>1</sup> Mast is used for nuts collectively, acorns, chestnuts, beechnuts, etc., especially when used as food for hogs and other animals.



## CYNIPS GALLÆ-TINCTORIÆ Olivier

The gall of *Cynips gallæ-tinctoriæ* Olivier, known in commerce as the Aleppo gall, Turkey gall, Levant gall, gall-nut, gall of commerce and ink marble, is found in eastern Europe, that is, in Hungary, Turkey and Greece, and in western Asia, on *Quercus ægilops*, *Quercus infectoria*, *Quercus pedunculata* and possibly *Quercus humilis*. This gall as an article of commerce has had the longest history, having been used from the time of the ancient Greeks to the present; has been used for the greatest variety of purposes; and has been considered as the richest of all the galls known to the Western World.

*Medicine.*—The earliest use of this gall was in medicine in which capacity it was known to the Greeks and to the Romans. In Greece it was recorded as of medical value by Hippocrates in the fifth century B.C. and then by Theophrastus, third century B.C. Its use by the Romans was treated at some length by Pliny, who stated that twenty-three remedies were compounded of gall-nuts, and that among the diseases for which they were used were ulcerations of the mouth, affections of the gums and uvula, malformed nails, hang nails, etc., and that for the relief of toothache and burns the inner part of the gall should be chewed.

From these early days until very recent times authors of *Materia Medica* have included this gall-nut as a drug, designating it as "the most powerful of vegetable strignents." In modern times it has been used in Europe as a cure for fevers and was especially popular in France early in the eighteenth century. At that time Poupart in *Mem. Ac. Sci.*, 1702, made a report on it which proved it to be of doubtful efficacy. Nevertheless its use was continued and as late as 1849 Pereira, in London, listed it as useful for medical purposes, recommending it as a tonic in intermittents, an astringent in hemorrhages, a chemical antidote, a topical astringent and giving a list of six medicines concocted from it. At the present time gall



products are found in the British Pharmacopœia as astringent ointments and in the U. S. Pharmacopœia, 1916, ninth revision, the Aleppo gall still appears as the source of tannic acid and as the principal ingredient in the preparation *Unguentum gallæ*. It is now used only externally.

*Ink.*—In the manufacture of ink the Aleppo gall was long considered as a necessary ingredient, especially where a durable ink was required, as in court records. In some places the law required that records be made with ink compounded of gall-nuts.

This use of the gall is not of such ancient origin as the medical use, for Pliny, who quotes the older authorities on other matters, has made mention only of the ink compounded of lampblack, which was used also by the Chinese. Hoefer in his "Histoire de la Chimie" spoke of an ink used in the third and fourth centuries A.D., compounded of acid and metal solution but failed to say that this acid was obtained from gall-nuts. The ink made from gall apple was, however, well known to the monks of the ninth and tenth centuries, who used it in copying their manuscripts. An interesting reference to the ink made from gall-nuts occurs in Scheffel's "Ekkehard," a romance of the tenth century, in which the monk Ekkehard says ". . . all ink comes from gall apples and all gall apples from a wicked wasp's sting." Of course, this is of interest only if the knowledge of the origin of the gall apple were part of the experience of the tenth-century monk and not supplied from the knowledge of the nineteenth-century author. As the search to clear up this point would be long and arduous and the result of no real value it has not been made.

From the ninth century down to the present day, gall-nuts have been included in practically every good ink recipe for black writing and record inks. The Aleppo gall is considered as the best for ink-making, but other important ones are the Morea gall, the Smyrna gall, Mar-mora gall and Istrian gall, and other good quality galls



from France, Hungary, Italy, Senegal and Barbary. The Chinese and Japanese galls are also sometimes mentioned in recipes. The Japanese gall has been used in making school and other cheap inks.

The Massachusetts Record Commission in 1891 made a Report on Record Inks and Paper in which the superiority of gall-nut ink was attested. The ink made from gall-nuts was said to be permanent, if properly made, and to have the advantage that if the writing should fade it could be repeatedly restored by a solution of nut-gall or tannin. Any other coloring matter substituted in whole or in part for gall-nut and iron solution impairs the quality of the ink.

In 1912, Oyster in the "Spatula Ink Formulary" gives as the basis of the best black writing and record inks, gall-nuts. In the recipes for inks used by the United States Treasury, Bank of England, the German Chancellory, and the Danish Government the Aleppo gall is specified.

Lehnen also states that nut-gall extract forms an excellent material for the preparation of ink, especially where manufacturers can not keep large stocks of the nut-gall itself. According to the 1917 annual report of the *Oil, Paint and Drug Reporter*, large quantities of gall-nut extracts are imported into the United States. Of course, all of it may not be used for ink manufacture.

*Tanning.*—Among tanning materials this gall-nut is the richest of all in the tanning principle and has been used, for tanning purposes, in the preparation of hides and skins, but because of its expense and its value to the textile colorist it has not been extensively used. Experiments and analyses of these galls were undertaken, however, with a view to discovering the tanning principle in vegetable matter. Pliny mentioned the preparation of leather as being one of the uses of gall-nuts, Bose recorded galls as being used in the tanning of hides and Davis in 1897 spoke of them as being the richest in tannin of all tanning materials, but made no further mention of



them in his descriptions of the processes of tanning. Other more recent writers on tanning materials have also listed oak galls,

*Dyeing.*—In the history of the art of dyeing, the Aleppo gall figures largely from the earliest mention of the art in literature up to the very present. According to Theophrastus it was used by the Greeks in dyeing wool and woollen goods and Pliny mentioned it as being used to stain the hair black and as the best adapted for the preparation of leather and the dyeing of skins. As the ancients could not conceive of a scholar's taking an active interest in the technical arts there is no record of how these galls were used, merely the statements that they were so used; and it was not until the end of the eighteenth century that any definite knowledge of these galls was sought.

It was at that time, when science invaded nearly every field of endeavor, that the chemists made an earnest effort to determine the chemical contents and action of gall-nuts, so as to place the arts of dyeing and tanning on a firmer and more scientific basis. Déyeux in 1793 was the first to separate the tannin in the gall-nuts and his experiments were followed up by Scheele, to whom is accredited the discovery of gallic acid. Berthollet and Fourcroy made more detailed analyses of the gall-nuts and gave more positive knowledge of the various properties and their chemical value.

Berthollet in "The Elements of the Art of Dyeing" gave perhaps the first scientific account of the art of dyeing with full explanations of methods and materials. According to his idea the great value of the Aleppo gall lay in its astringency and as it is most astringent before the insect escapes, the immature galls, or as they are called, the blue galls, are of the most value and are the ones used in dyeing black, while the white galls, or those from which the insect has escaped, are used in dyeing light linens. For the dyeing of black Berthollet considered that no



other astringent than an infusion of gall-nuts could be used in the dyeing bath, as too large a quantity of any other material would be necessary to obtain the same results.

Bancroft, however, in his "Philosophy of Permanent Color," 1813, opposed the idea that the astringency was the important property of the gall-nut and set forth the idea that it should be considered merely as a coloring matter. In defense of his theory he showed that tannin procured from different vegetable matter and combined with iron will not produce black, and gallic acid alone will not blacken solutions of iron, while either tannin or gallic acid from *galls* combined with iron forms a black dye or ink.

At the present time both these theories are known to be true for the Aleppo gall may be used as a fixing agent in dyeing or may be used as the basis of a good black dye. As a dye its use appears to be confined to the dyeing of leather and of sealskin fur.

In the dyeing of leathers and skins the Aleppo gall is used in small quantities with other dyeing materials to obtain the best and most permanent black. That the successful dyeing of leathers, however, is not dependent entirely upon a good dye is evident from the following statement on leather dyeing by Bennett, "Manufacture of Leather," 1909:

The absorption of the dye by the fiber has been considered a case of chemical action, of physical action and even as a case of "solid solution," but it is highly probable that more than one type of action comes into play and that possibly all these theories may be true to a certain extent. It would, however, appear that with vegetable tannages the determining factor is the formation of color lakes with the tannin on the fiber. The tannins are of an acid nature and fix the basic dyes with great readiness, but the basic chrome-tanned leathers fix the basic dyes much less readily than the acid dyes, so it is clear that the nature of the tannage has considerable influence in the matter.

For the dressing and dyeing of sealskin furs, large quantities of the Aleppo galls were formerly shipped to



London, where all of our American sealskins were dressed and dyed for the market. Now, however, this industry has been established in the United States, and in 1914 gall-nuts worth \$17,174 were imported from Bagdad for this purpose. As the method of dyeing sealskins is a very jealously guarded trade secret the American firm engaged in this enterprise has had to work out its own processes, and according to the Commerce Reports this has been successfully accomplished and one sale of American sealskins dressed and dyed in America has taken place, in St. Louis, in September, 1916.

*Analysis.*—A gall so widely known and of such great value has of course been analyzed many times and is the standard for the analysis of others. According to Trimble the most generally accepted analysis is that made by Guibort, which is as follows:

	Per Cent.
Tannic acid .....	65
Gallie acid .....	2
Ellagic acid	2
Luteo-gallie acid }	
Chlorophyll and volatile oil .....	0.7
Brown extractive matter .....	2.5
Gum .....	2.5
Starch .....	2
Woody fiber .....	10.5
Sugar	1.3
Albumen	
Potassium sulphate	
Potassium gallate	
Gallate of lime	
Oxalate of lime	
Phosphate	
Moisture .....	11.5
	100.00

#### CYNIPS INSANA Westwood

A gall somewhat resembling the Aleppo gall and often confused with it is that produced by *Cynips insana* Westwood. It is better known as the mad apple of Sodom, Dead Sea fruit, or Mecca or Bussorah gall, and is found in Palestine, Asia Minor, Albania and Italy on *Quercus*



*infectoria*, *Quercus tauricola* and *Quercus farnetto* (*conferta*). Its use is confined to the locality from which it takes one of its names, Bussorah or Basra.

This gall has furnished an interesting and somewhat mystifying theme to poets and has been often discussed by old writers who have tried to connect this so-called fruit with some of the unknown fruits mentioned in the Bible.

In Bussorah or Basra in Asia Minor, probably its native heath, this gall is used by the inhabitants in dyeing Turkey red, and it is more esteemed by them than the Aleppo gall.

*Analysis.*—The following analysis of this gall was made by Bley in 1853:

	Per Cent.
Tannic acid .....	26.00
Gallie acid .....	1.60
Fatty oil .....	0.60
Resin .....	3.40
Extractive and salts .....	2.00
Starch .....	8.40
Woody fiber .....	46.00
Moisture .....	12.00
	<hr/> 100.00

#### CYNIPS QUERCUS-CALYCIS Burgsdorf

The knopperrn or acorn gall, also called the Piedmontese gall, and gall of Hungary, which is produced on *Quercus agrifolia*, *Quercus pedunculata* and occasionally on *Quercus pubescens* and *Quercus sessiliflora*, occurs in Austria, Hungary, Slavonia, Bosnia, Serbia, Greece, Asia Minor and less abundantly in Germany, Holland, France and Italy. Among the Cynipid galls it ranks next in importance to the Aleppo gall and has been almost as frequently discussed.

In Austria it has been used chiefly by the tanners, but has also been substituted by dyers for the Aleppo gall. This gall, like the Aleppo, is at its best before maturity and should be collected from August to October.



At its height the Knopperrn yields from 45 to 50 per cent. of tannin.

#### CYNIPS KOLLARI Hartig

The Devonshire gall is produced by *Cynips kollari* on *Quercus avellanae-formis*, *Quercus fastigiata*, *Quercus humilis*, *Quercus ilex*, *Quercus lusitanica* and varieties, *Quercus mirbeckii*, *Quercus mongolica*, *Quercus pedunculata* and varieties, *Quercus pubescens*, *Quercus pseudoægilops*, *Quercus rubra*, *Quercus sessiliflora*, *Quercus suber* and *Quercus toza*. It occurs in middle and southern Europe, North Africa, Asia Minor, and was introduced into England from the continent early in the nineteenth century. It attracted much attention because of its rapid spread, but the interest in it seems to have been confined to England, as no important reference to it has been found elsewhere.

Attention was first drawn to this gall in England, when it became so abundant that the extermination of the oak forests seemed threatened by it. At that time, about 1858, many notices concerning it appeared in which fear was expressed that it would do irreparable injury to the oaks. But the damage done by it was of no great moment and when the gall was studied it was found to have some tanning and dyeing properties, and to be useful in making an excellent ink.

Many analyses were made of this gall in which varying amounts of tannin were accredited to it. The following was made in 1869 by Watson Smith:

	Per Cent.
Tannic acid .....	26.71
Gallie acid .....	Traces only
Woody fiber .....	47.88
Moisture .....	20.61
Coloring and loss .....	4.80
	<hr/> 100.00

#### RHODITES ROSÆ Linnæus

The Bedeguar of the rose, the gall produced by *Rhodites rosæ* Linnæus, occurs throughout Europe and in western



Asia on eighteen species of *Rosa*, and in North America on *Rosa canina* only. It was highly esteemed by the ancients, but has received very little mention in more modern times as being of any particular use to man.

This gall was mentioned by Pliny as being among the most successful applications for the restoration of hair. For this purpose it had to be powdered and mixed with honey. In Italy it has been used, when powdered and laid on the affected parts, to cure the bite of venomous creatures. This use by the Italians may have grown out of the story related by Pliny that the mother of one of the prætorian guard had a dream, after her son had been bitten by a mad dog, in which she was directed to procure the little round balls at the root of the wild rose and apply them to the affected part. Cuvier has recorded the Bedeguar of the rose as among the remedies successfully used against diarrhœa, dysentery, and cases of stones, scurvy and worms, and as late as 1868 the farmers near Harrogate were known to gather the mossy galls of the rose to make an infusion for diarrhœa in cows, for which they claimed to find it very successful.

#### AULAX sp. Rübsaamen

The gall of the sage or "Pomme de sauge" is produced by *Aulax* sp. Rübsaamen on *Salvia pomifera* and other species of *Salvia* in the Isle of Crete.

The earliest available record of the use of these galls is that by Belon in 1558 in which he described them as being large as galls, covered with hair and sweet and pleasant to the taste. They were collected at the beginning of May and sold by the people of Candie to neighboring villagers. Olivier stated that "they are esteemed in the Levant for their aromatic and acid flavor, especially when prepared with honey and sugar, and form a considerable article of commerce from Scio to Constantinople, where they are regularly exposed in the market."



Fockeu in 1897 mentions having found these galls in the East but states that to-day the old common name, Baisonge, is unknown and that the people of the country when questioned concerning them said that they had never noticed their existence and expressed doubt of their ever having been used for food, or in making confections.

This name "Baisonge" was not used by either Belon or Olivier for the gall of the sage, but has been used by Cuvier to designate a terebinthe gall from Syria.

#### AULAX GLECHOMÆ LINNÆUS

Another Cynipid gall which has been used as food is the gall of the ground ivy made by *Aulax glechomæ* on *Glechoma hederacea* L. It occurs in Lorraine and Sweden.

This gall was used in France as food and is said to have an agreeable taste and the sweet odor of the host-plant.

#### CHINESE OAK GALL

An unidentified oak gall, said to closely resemble the European gall, is one which was recorded in Pen T'Sau as Woo-shih-tsze.

The following translation of the note concerning it has been published by Pereira (*Pharm. Journ.*, Vol. 3, 1844, pp. 384-7):

Woo-shih-tsze also comes from the West, and from India. The tree is said to be sixty or seventy cubits high and eight or nine cubits in circumference, and grows in sandy and stony places. It is compared . . . to the camphire tree. It flowers in the third moon; the flower is white, and rather red in the center. The bud formed is round like a ball; at first green—when ripe, yellowish. An insect eats into it and forms a hole in it. They say that the tree one year produces the Woo-shih-tsze, and another year produces something which resembles a chestnut.

Another name is Whi-ztsip-tsze. It has various medicinal properties. It is used with some other ingredients for dyeing beards black.

The taste of the Woo-pei-tsze is, according to them, a sour, saltish taste—of the Woo-shih-tsze, a bitter taste.



In the *Materia Medica* of China (Smith, 1871, p. 100) it is called "food for the foodless" and is recommended for medicinal use. It is said to differ little from those of the European market and to have been used formerly in making ink and in dyeing hair.

As this gall is described by the Chinese as coming from the "West" could it possibly be the Aleppo gall, the distribution of which is eastern Europe and western Asia?

#### SCHLECHTENDALIA CHINENSIS (Bell)

Besides the Cynipid galls many others have been recorded as of use to man. Most of them are merely included in the native *Materia Medica* of China and India, but a few have had other uses.

The most important of these galls is the Chinese gall or Woo-pei-tsze, produced by *Schlechtendalia chinensis* on *Rhus semialata*, in northern India, China and Japan. It has been known and used by the Chinese for many centuries, perhaps even longer than the Aleppo gall has been known in the West. It rivals the Aleppo gall in importance and like the latter is still an important article of commerce.

The Chinese gall has been used in medicine, tanning, and dyeing, and is now imported into Germany and the United States for the manufacture of tannic acid, of which it yields about 70 per cent. As this gall has been fully treated in a paper by A. C. Baker, which has been submitted for publication it is unnecessary to give details here.

#### CHERMES sp. (Baker)

The gall identified by Kirby and Spence as that of *Aphis pini* has been identified by Mr. A. C. Baker as *Chermes* sp., possibly *Chermes lapponicus* Chol, possibly some other. It occurs on spruce-fir in Lapland.

Linnaeus states that this gall was used as food, and



Kirby and Spence suggested it as a possible dyeing material. Linnæus's description of it is as follows:

The extremities of the branches of the spruce-fir bear small yellow cones. . . . When arrived at maturity they burst asunder and discharge an orange-colored powder which stains the clothes of those who approach the tree. I conceive these excrescences to be caused by some minute insects. The common people eat them raw as a dainty, like berries.

It was probably the reference to the orange-colored powder staining the clothes which led Kirby and Spence to suggest that this gall might be placed among dyeing materials.

#### PEMPHIGUS CORNICULARIS

The gall of *Pemphigus cornicularis*, called in India, Kakra-Singhee, in Syria, Baizonge, and in Europe, gall of the terebinth, occurs in southern Europe and Turkey, in Spain, Syria, China and India.

In India this gall is used in medicine by the natives who assign to it great astringent and tonic properties.

The Hindus have also used it, to a limited extent, in dyeing.

In Thrace and Macedonia Belon recorded it as being collected at the end of June, while still immature, and sold at high prices to the inhabitants of Bource, who used it in coloring fine silks. In Spain, Syria and China it was used as an ingredient in making scarlet dye.

#### ALDACAY GALLS

Galls called Aldacay or Caducay galls were recorded by Roxburgh in 1805 as occurring on the leaves of *Mimosa arabica* on the coast of Coromandel. Kirby and Spence in speaking of this gall called the host-plant *Terminalia citrina*.

These galls were said to have been among the most valued of the native dyeing materials and to have been sold in every market. The natives dyed their best and



most durable yellow with them, and they were also used by the chintz painters for their yellows. When mixed with ferruginous mud a strong black dye was obtained.

The astringent properties of these galls were evidently stronger than those of the fruit of the tree, as an ink made from the galls resisted the weather longer than that made from the fruit.

Roxburgh did not identify these galls, but suggested that they might be the "Faba bengalensis" of the old Materia Medica writers. The "Faba bengalensis" according to Bose is the fruit of the *Myrobolan citrin* altered in its form by the puncture of an insect, but no dyeing properties are ascribed to it. As no further reference to these galls has been found they are still undetermined.

#### SUMMARY

The important uses of galls have been in medicine, the manufacture of ink, tanning and dyeing, with a few references to their use as food, and one to their use as fuel.

In medicine the following galls have been used: *Andricus fecundatrix* Hartig, *Cynips* sp. Cuvier on field cirsium, *Cynips gallæ-tinctoriæ* Olivier, *Cynips polycera* Giraud, *Cynips quercus-folii* Linnæus (*Cynips quercus-terminalis*) = *Biorhiza pallida* Olivier, *Cynips quercus-tozæ* Bose, *Pemphigus cornicularis*, *Pemphigus pallidus*, *Rhodites rosæ* Linnæus, *Schlechtendalia chinensis* (Bell) and the undetermined ones: Chinese oak gall, Istrian gall, Marmora gall, galle corniculée, and Bazgendge (Fockeu) or Chersamel on *Tamarix*.

In the manufacture of ink the galls used are: *Cynips gallæ-tinctoriæ* Olivier, *Cynips kollari* Hartig, *Schlechtendalia chinensis* (Bell), the Aldacay or Caducay galls, the Istrian, Marmora, Morea and Smyrna galls and others from France, Italy, Hungary, Senegal and Barbary.

For tanning the following have been found useful: *Cynips gallæ-tinctoriæ* Olivier, *Cynips hungarica* Hartig, *Cynips insana* Westwood, *Cynips kollari* Hartig, *Cynips*



*lignicola* Hartig, *Cynips quercus-calycis* Burgsdorf and *Schlechtendalia chinensis* (Bell).

For use in dyeing have been recorded: *Cynips gallæ-tinctoriæ* Olivier (*Cynips tinctoria-nostra*) = *Cynips infectoria* Hartig, *Cynips insana* Westwood, *Cynips kollari* Hartig, *Cynips quercus-calycis* Burgsdorf, *Cynips quercus-petiolis* Linnæus, *Pemphigus cornicularis*, *Schlechtendalia chinensis*, possibly *Chermes* sp. Baker, and the undetermined galls, Aldacay or Caducay galls, the gall-nut used by the Somali women for a tattooing dye, Baizonge Cuvier and Bazdyendge Pomet.

As food, only a few galls have been used: *Aulax* sp. Rübsaamen or Baisonge Fockeu, *Aulax glechomæ*, *Cynips* spp. Girault, *Disholcaspis weldi* (Beutenmüller), *Calirhytis* sp.? Hopkins, *Chermes* sp. Baker and *Schlechtendalia chinensis*. In the case of the last named the gall itself is not eaten but the powder found on the outside is used for seasoning soup.

As fuel for lamps the Greeks used *Cynips theophrastea* and an undetermined gall called by Pliny the black-gall-nut.

#### COMMON NAMES OF INSECT GALLS

In the following list of the common names of the insect galls which have been of any practical use, will be found a number of names for the gall of *Cynips gallæ-tinctoriæ* and several for that of *Schlechtendalia chinensis*. To avoid confusion I would suggest that for the former the name Aleppo gall be adopted, and for the latter the name Chinese gall, as it is under these names that they are designated in the commerce reports, in some of the trade journals and in the technical works on dyeing, tanning and ink manufacture.

Acorn gall .....	<i>Cynips quercus-calycis</i> Burgsdorf
Aleppo gall .....	<i>Cynips gallæ-tinctoriæ</i> Olivier
Baisonge Fockeu .....	<i>Aulax</i> sp. Rübsaamen
Baizonge Cuvier .....	<i>Pemphigus cornicularis</i>
Bara Mai .....	Hindu name of a gall on <i>Tamarix gallica</i>



- Bazdyendge Pomet ..... Turkish name for a gall on oak  
 Bazgendge Fockeu ..... Turkish name for a gall on *Tamarix orientalis*  
 Bedequar of the rose ..... *Rhodites rosæ* Linnaeus  
 Black gall-nut Pliny ..... Undeterminable  
 Black oak wheat ..... *Callirhytis* sp.? Hopkins  
 Bussorah gall ..... *Cynips insana* Westwood  
 Chersamel ..... Egyptian name for Bazgendge (q.v.)  
 Chinese gall ..... *Schlechtendalia chinensis* Bell  
 Chinese pear gall ..... *Schlechtendalia chinensis* Bell  
 Chota Mai ..... Hindu name for a gall on *Tamarix orientalis*.  
 Dead Sea fruit ..... *Cynips insana* Westwood  
 Devonshire gall ..... *Cynips kollari* Hartig  
 Fruits for the foodless ..... A Chinese oak gall  
*Faba bengalensis* ..... A gall on *Terminalia chebula*  
 Gall of commerce ..... *Cynips gallæ-tinctoriæ* Olivier  
 Gall of field cirsium ..... *Cynips* sp. Cuvier  
 Gall of sage ..... *Aulax* sp. Rübsaamen  
 Gall of *Mimosa arabica* Roxburgh .? *Faba bengalensis*  
 Gall-apple ..... *Cynips gallæ-tinctoriæ* Olivier  
 Gall-nut Burton ..... Undeterminable  
 Galle de France ..... *Cynips kollari* Hartig  
 Galle en artichaut ..... *Andricus fœcundatrix* Hartig  
 Galle corniculée Guibort ..... Undeterminable  
 Gul-i-pista ..... *Pemphigus pallidus*  
 Hungary gall ..... *Cynips quercus-calycis* Burgsdorf  
 Ink marble ..... *Cynips gallæ-tinctoriæ* Olivier  
 Istrian gall ..... Undeterminable  
 Japanese gall ..... *Schlechtendalia chinensis* Bell  
 Kakra Singhee ..... *Pemphigus cornicularis*  
 Knopperr ..... *Cynips quercus-calycis* Burgsdorf  
 Levant gall ..... *Cynips gallæ-tinctoriæ* Olivier  
 Mad apple of Sodom ..... *Cynips insana* Westwood  
 Marmora gall ..... Undeterminable  
 Mecca gall ..... *Cynips insana* Westwood  
 Nut-gall ..... *Cynips gallæ-tinctoriæ* Olivier  
 Nut-gall ..... *Schlechtendalia chinensis* Bell  
 Oak apple ..... *Andricus quercus-californicus*  
 Oak-apple galls ..... *Cynips* spp. Girault  
 Oriental gall ..... *Cynips gallæ-tinctoriæ* Olivier  
 Piedmontese gall ..... *Cynips quercus-calycis* Burgsdorf  
 Pomme de chene Guibort ..... Undeterminable  
 Small crown gall of Aleppo ..... *Cynips polycera* Giraud  
 Sumrat-ül-asl ..... Arabic name for *Chota Mai* (q.v.)  
 Sumrat-ül-túrfa ..... Arabic name for *Bara Mai* (q.v.)  
 Turkey gall ..... *Cynips gallæ-tinctoriæ* Olivier  
 Wheat mass [Mast] ..... *Callirhytis* sp.? Hopkins  
 Whip-ztsip-tze and Woo-shih-tsze . A Chinese gall on oak  
 Wu-peï-tsze ..... *Schlechtendalia chinensis* (Bell)



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